The effects of oiling and rehabilitation on the breeding productivity and annual moult and breeding cycles of African Penguins

by

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Abstract

The de-oiling of contaminated seabirds has generally been viewed as having little conservation value. In this thesis I assessed the conservation value of de-oiling contaminated African Penguins *Spheniscus demersus*, by investigating the extent to which de-oiled birds are restored (i.e. resumed breeding after release) into the population. The study was carried out in the Western Cape, South Africa, between 1994 and 2005, and focused on the penguins de-oiled after the *Apollo Sea* oil spill of 1994 in which 10 000 penguins were oiled and the *Treasure* oil spill of 2000 in which 19 000 penguins were oiled and an additional 19 500 un-oiled birds were evacuated from Dassen and Robben Islands and transported to Cape Recife in the Eastern Cape to prevent them from becoming oiled. Systematic searches were carried out at Dassen Island over a period of 10.5 years to re-sight and record the activities of flipper-banded penguins that had been de-oiled. I use modern statistical tools that account for recapture probabilities, transience, and temporary absence from the breeding colonies. In total, 73% of the de-oiled penguins from the *Apollo Sea* oil spill that were re-sighted at Dassen Island were estimated to have been restored. This represents the most successful restoration of any seabird globally. However, the mean proportion of de-oiled breeders which abstained from breeding each year was about double the expected proportion. Moreover, there was a negative relationship between breeding and subsequent survival and breeding, suggesting a cost of reproduction for de-oiled birds. Between 2000 and 2005, a significantly greater proportion of evacuated birds from the *Treasure* oil spill were restored into the breeding population than de-oiled birds from the same spill. Lightly-oiled birds that were not caught and de-oiled had a lower restoration success than de-oiled birds, highlighting the value of de-oiling birds, even if they are only slightly oiled. Consistent with the finding for *Apollo Sea* birds, reproduction exerted a greater cost to de-oiled birds than to un-oiled evacuees.

Between 1994 and 2000, 18 breeding success studies were conducted at Dassen Island to compare the reproductive output of de-oiled birds from the *Apollo Sea* spill with un-oiled birds. In 13 of these studies, the growth rates of chicks from these two groups were compared. I used generalized linear models to investigate the influence of explanatory variables on both reproductive output and chick growth. Breeding success and chick growth rates were variable during the study period. Breeding success was higher than

previously reported figures for the species, and was correlated with the biomass of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax*. The overall breeding success of de-oiled birds was significantly lower than un-oiled birds. The lower reproductive output of de-oiled birds was due mainly to the reduced number of chicks which fledged, rather than poorer hatching success. Nests with two de-oiled *Apollo Sea* parents had a lower reproductive output than nests with one de-oiled bird. Chicks from nests with two de-oiled *Apollo Sea* parents had significantly slower growth rates than chicks from nests with one or no de-oiled parents. I suggest that the main reason for the poorer reproductive performance of de-oiled birds relates to their reduced ability to provision chicks, especially during the period of peak energy demand, and when feeding conditions deteriorate. De-oiled birds had a lower rate of mate fidelity than un-oiled birds, and there was a positive association between mate fidelity and breeding success.

The breeding and moult phenology of African Penguins at Dassen Island was investigated between 1994 and 2006. Moult was the most synchronous aspect of the annual cycle, and I suggest that it is the timing of moult, rather than breeding, which is the critical component driving the annual cycle. The seasonal pattern of moult at Dassen Island was similar to the pattern at Robben Island, but the degree of synchrony in moult was greater at Robben Island. The pattern of breeding of de-oiled birds following their release conformed to the overall pattern of the colony in which they bred. However, the *Apollo Sea* and *Treasure* spills disrupted the moult pattern of penguins at Dassen and Robben Islands for a period of up to two years following the spill.

Despite the negative impacts of the *Apollo Sea* and *Treasure* oil spills, which include the mortality of birds, substantial disturbance at the affected colonies during the rescue operation, and reduced breeding by de-oiled birds, the breeding populations at Dassen and Robben Islands increased after both of these spills. These increases were attributed to the increase in the abundance of their main prey, and would have been even greater had the spills not taken place. Since 2004, the number of active breeders has declined. In addition, the number of adult penguins counted moulting has decreased by 55% between 2003 and 2005 at Robben Island and by 50% between 2002 and 2005 at Dassen Island. These changes have coincided with an eastward shift in the distribution of their prey, reducing their availability to African Penguins at Robben and Dassen Islands.

De-oiling of African Penguins is considered to be a crucial conservation tool for a species which is classified as "Vulnerable" to extinction, and faces a number of other threats. However, the primary conservation aim should be the prevention of oil spillage, especially in the vicinity of seabird colonies and foraging areas.

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Chapter One

General Introduction

General Introduction

AFRICAN PENGUINS IN RELATION TO OTHER SPECIES IN THE GENUS *SPHENISCUS*

The African Penguin *Spheniscus demersus* is one of the four species in the genus *Spheniscus*. It is the only resident penguin found along the African coast, and is endemic to the Benguela upwelling system off southern Africa, which extends from southern Angola in the north to about Algoa Bay in the east (Crawford *et al.* 2006). The African Penguin, previously referred to as the Jackass, Cape or Black-footed Penguin, is morphologically similar to the Humboldt *S. humboldti* and Magellanic *S. magellanicus* Penguins of South America, and their status as separate species has been queried by some (Clancey 1966, Grant *et al.* 1994). The fourth member of the genus, the Galápagos Penguin *S. mendiculus*, differs sufficiently in appearance from the other three species that its species status has never been questioned. *Spheniscus* penguins are largely allopatric, although the ranges of the Humboldt and Magellanic Penguins overlap in northern Chile (Wilson *et al.* 1995).

The Magellanic Penguin, the most closely related to the African Penguin (Grant *et al.* 1994), breeds around the southern tip of South America from 40°S in Argentina to 37°S in Chile, and on the Falkland Islands (Williams 1995, Wilson *et al.* 1995). The Humboldt Penguin is endemic to the Humboldt Current, and its breeding range extends from 5°S in Peru to 37°S in Chile (Williams 1995, Wilson *et al.* 1995). The Galápagos Penguin is the northernmost of all penguins. It is endemic to the Galápagos Islands, where it mainly breeds on Fernandina and Isabela Islands (on the equator), which are located within the major upwelling zones of the Cromwell Current (Boersma 1976, 1978, Vargas *et al.* 2006). The timing of breeding is more flexible in *Spheniscus* penguins than in any other group of penguins. Of the four species in the genus, the Magellanic Penguin is the only strictly seasonal breeder; it is also the only migratory, offshore-foraging species in the genus (Boersma *et al.* 1990, Frere *et al.* 1998, Croxall & Davis 1999, Yorio *et al.* 2001). African, Humboldt and Galápagos Penguins tend to remain at or near their breeding colonies throughout the year, but, especially in the case of African and Humboldt Penguins, may at times travel large distances (Culik & Luna-Jorquera 1997, Culik *et al.*

2000, Whittington *et al.* 2005). The four species of *Spheniscus* penguins are the most tropical of the penguin genera, and constitute the northern end of the distribution of penguins. Consequently, they breed in warmer climates than most other penguins. As a result all four species prefer breeding in burrows, within rock crevices and caves, or under shrubs (Boswall & MacIver 1975, Boersma 1976, Frost *et al.* 1976a, b, Paredes & Zavalaga 2001). The timing of moult is also more variable within *Spheniscus* penguins compared with other penguin genera. Magellanic Penguins moult relatively synchronously after the breeding season (Boersma *et al.* 1990). Galápagos Penguins moult prior to the onset of breeding, often within one to four weeks of initiating a breeding attempt; they also moult more frequently (on average, twice a year) than the other *Spheniscus* penguins, which generally moult once a year (Boersma 1976). African and Humboldt Penguins can moult either before or after breeding (Cooper 1978, Paredes *et al.* 2002, Simeone *et al.* 2002), a feature which is likely to be related to the extended breeding season of these species.

Although *Spheniscus* penguins breed in warmer climates than other penguins, their breeding areas are generally associated with upwelling current systems that are characterised by high primary production and historically large stocks of pelagic fish (Boersma 1976, 1978, Shannon & Pillar 1986, Crawford *et al.* 1987, 2006, 2007). This is especially the case for the three inshore-foraging species of the genus, the African, Humboldt and Galápagos Penguins, which are associated with the Benguela, Humboldt and Cromwell upwelling systems, respectively. The Humboldt and Cromwell systems experience a higher frequency of environmental perturbations, such as El Niño Southern Oscillation (ENSO) events, than the Benguela system (Duffy *et al.* 1984, Hays 1986, La Cock 1986, Valle *et al.* 1987, Boersma 1998a, Crawford *et al.* 2006). The increase in the sea surface temperature associated with ENSO events results in reduced upwelling and productivity, which ultimately limits the food available to penguins within these systems. Consequently, ENSO events have significantly depressed the populations of Galápagos (Valle *et al.* 1987, Boersma 1998a, b, Vargas *et al.* 2006) and Humboldt Penguins (Hays 1986, Paredes & Zavalaga 1998, Culik *et al.* 2000, Simeone *et al.* 2002). In the Benguela system, Benguela Niños also cause a greatly reduced availability of fish to seabirds in Namibia (Boyer & Hampton 2001), but occur much less frequently than the ENSO events of the other two systems (Binet *et al.* 2001, Roux 2003), and so have not depressed African Penguin populations to the same extent as the other two species.

DISTRIBUTION AND STATUS

The African Penguin currently breeds at 31 sites between Hollams Bird Island, off central Namibia, and Bird Island, Algoa Bay (Crawford *et al.* 2007) (Figure 1.1). The breeding range can be broadly divided into three regions: southern Namibia, the Western Cape and the Eastern Cape (Figure 1.1). Non-breeding birds disperse from southern Angola (Brooke 1981) to KwaZulu-Natal (Wilkinson *et al.* 1999), with vagrants recorded as far north as Gabon in the west and Mozambique in the east (Crawford & Whittington 1997). At least 12 African Penguin breeding colonies are known to have become extinct (Crawford *et al.* 1995a, b, Kemper 2006). Two former breeding localities have been re-colonised: Robben Island in 1983 (Crawford *et al.* 1995c) and Neglectus Islet in Namibia in 2001 (Roux *et al.* 2003). Two mainland sites in South Africa were colonised in the 1980s, Stony Point in 1982 (Broni 1982) and Boulders Beach in 1985 (Cooper 1985, Crawford *et al.* 2000a). In addition a new penguin colony was established on the mainland coastline at De Hoop Nature Reserve, near Cape Agulhas in 2003 (Underhill *et al.* 2006). In total, 26 of the extant breeding colonies are located on offshore islands or rocky outcrops, although Marcus Island in Saldanha Bay and Bird Island in Lambert's Bay were connected to the mainland by causeways in 1976 and 1959, respectively (Shelton *et al.* 1984, Cooper *et al.* 1985, du Toit *et al.* 2004). In both cases, the causeways facilitated access to these islands by terrestrial predators and thus increased predation on penguins and other seabirds occurred (Cooper *et al.* 1984). The other five breeding localities comprise mainland sites, three in South Africa, and two in Namibia. At the Namibian mainland colonies, penguins breed in caves located at the base of vertical cliffs (Bartlett *et al.* 2003, Simmons & Kemper 2003).

POPULATION TRENDS

The African Penguin declined markedly in numbers during the 20th Century. The earliest estimates of any African Penguin population were of the colony at Dassen Island. A lighthouse keeper at Dassen Island reported that in February 1906 there were nine million penguins present on the island (Shannon & Crawford 1999). Kearton (1930)

claimed that there were at least five million penguins at Dassen Island during his visit in the 1920s (Figure 1.2). However, these figures were considered to be overestimates (Westphal & Rowan 1971, Frost *et al.* 1976b), and Westphal & Rowan (1971) estimated that there were 1.5 million penguins on Dassen Island between 1900 and 1930. The first reliable estimates of the African Penguin population were made using aerial photographs in 1956 (Rand 1963a, b). The total population size of African Penguins in 1956 was estimated to be 296 000 adult birds (Rand 1963a, b). The population declined to about 220 000 birds by the late 1970s (Crawford *et al.* 1990). During the early 1990s the population was estimated to be about 179 000 adult penguins and declining at a rate of 2% per year (Crawford *et al.* 1995b, Ellis *et al.* 1998, Whittington *et al.* 2000). There was a slight recovery in the late 1990s, especially at colonies in the Western Cape (Wolfaardt *et al.* 2001, Underhill *et al.* 2006, Crawford *et al.* in prep.). The estimated population in 2000 was about 201 000 adult penguins (Hockey *et al.* 2005), some 13% of the estimated number at the beginning of the 20th century.

As a consequence of the rapid decline of the African Penguin population, it has been classified as "Vulnerable" in the South African Red Data Book of birds since 1984 (Brooke 1984, Barnes 2000) and is considered "Vulnerable" in terms of the IUCN classification (BirdLife International 2004). The reasons for the decrease in numbers have been well documented. The main factors implicated in the decline during the early part of the 20th century were related to human activities at breeding colonies. The commercial value of seabird guano as an agricultural fertiliser led to the large-scale collection of guano at South African and Namibian Islands from 1843 (Best *et al.* 1997). Guano-scraping activities caused severe disturbance to nesting seabirds, reducing their breeding success and thus recruitment into the breeding populations (Rand 1970, Berry *et al.* 1974, Frost *et al.* 1976b, Cooper 1980). In addition, it compromised the quality of nesting habitat for African Penguins. After the guano had been removed, penguins at many of the affected colonies were forced to nest on the surface, where they are more susceptible to disturbance, predation, and heat stress. Consequently, the breeding success of penguins nesting on the surface is significantly lower than those breeding in burrows (Frost *et al.* 1976b, Cooper 1980, Murison 1998, Kemper 2006). The large scale collection of penguin eggs was another critical factor which contributed towards the initial decline of penguin numbers, especially from about 1900 to 1930. During this period in excess of 450 000 penguin eggs were collected annually from Dassen Island alone (Cott

1953, Frost *et al.* 1976b, Siegfried & Crawford 1978), substantially reducing recruitment into the population (Frost *et al.* 1976b). The collection of penguin eggs for human consumption, along with the collection of birds for their oil, may have led to the extinction of the former African Penguin colony at Robben Island prior to 1800 (Westphal & Rowan 1971). Egg collecting activities formally ceased in 1967 (Shelton *et al.* 1984), and in South Africa guano harvesting was terminated in 1984 (du Toit *et al.* 2004).

Currently, the main threats to African Penguin populations are experienced at sea rather than at the breeding colonies. African Penguins feed largely on shoaling epipelagic fish, predominantly Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax* (Hockey *et al.* 2005). Patterns in the abundance of penguins are associated with the abundance and distribution of these forage fish (Crawford 1998, 1999, Crawford *et al.* 2001). Commercial purse-seine fisheries developed rapidly off South Africa and Namibia from the 1950s and competed with African Penguins and other marine predators for these fish species. This resulted in the reduced availability of pelagic fish prey for African Penguins (Randall & Randall 1986, Crawford 1998, Crawford *et al.* 2001), especially in Namibia, where the Sardine stock collapsed in the early 1970s (Boyer & Hampton 2001). Consequently, the number of penguins breeding in southern Namibia decreased from 40 000 pairs in 1956 to approximately 1 000 pairs in 2000 (Crawford *et al.* 2001). Off South Africa, the collapse of the Sardine stock is thought to have caused the large decreases in penguin populations to the north of Table Bay between 1956 and 1980 (Crawford & Shelton 1981, Crawford 1998, Crawford *et al.* 2001). Subsequently, changes in the distribution and relative abundance of Anchovy and Sardine off South Africa (Barange *et al.* 1999, 2004, van der Lingen *et al.* 2005, Fairweather *et al.* 2006) have been associated with fluctuations in the sizes of the penguin populations in the region (Crawford 1998, Wolfaardt *et al.* 2001, Underhill *et al.* 2006).

In addition to the impacts of commercial pelagic fisheries and the variable patterns of abundance and distribution of Anchovy and Sardine, African Penguins also compete with other marine predators, such as the Cape Fur Seal *Arctocephalus pusillus*, for these fish stocks. Cape Fur Seal populations increased throughout the 20th century, particularly after the 1940s (Butterworth *et al.* 1995, Crawford *et al.* 2001), and so the interactions between Cape Fur Seals and African Penguins have become more intense (David *et al.* 2003). Cape Fur Seals also compete with African Penguins and other

seabirds for breeding space at island colonies (Shaughnessy 1980, Crawford *et al.* 1989), and are predators of African Penguins (Marks *et al.* 1997, Crawford *et al.* 2001, David *et al.* 2003). Although not a significant mortality factor at the population level, African Penguins often die when they become entangled in discarded fishing gear and other marine debris (Wolfaardt 1999).

Currently, oil pollution constitutes one of the major threats to African Penguin populations (Whittington *et al.* 2000, Nel & Whittington 2003). Because they are flightless, penguins are not able easily to avoid oil slicks, and are thus particularly susceptible to oil pollution events. The first documented oil spill affecting African Penguins occurred in 1948 (Green 1950). The rate of oiling and the number of penguins affected has increased substantially since then, especially after 1990, largely due to two oil spills which contaminated approximately 30 000 African Penguins: the *Apollo Sea* spill in 1994 (Barrett *et al.* 1995, Underhill *et al.* 1999), and the *Treasure* spill in 2000 (Crawford *et al.* 2000b, Kuyper & Williams 2004). Although these catastrophic spills affect larger numbers of birds than chronic pollution events, the cumulative impact of chronic oiling also constitutes a critical threat to African Penguin populations (Shannon & Crawford 1999, Ryan 2003).

DASSEN ISLAND – STUDY SITE, AND BRIEF HISTORY OF HUMAN ACTIVITY

Dassen Island is situated approximately 55 km north west of Cape Town (33°25'S, 18°06'E, Figure 1.1). The island is 220 ha in size; it is the second largest South African continental island, after Robben Island, which is 507 ha (Crawford *et al.* 1995c). The island is flat and low-lying, the highest point above sea level being only 19 m (Wolfaardt 2000). The island is formed on a granite base and is predominantly sandy with patches of exposed rock mainly along the shore. The geology of the island comprises predominantly fine-grained tourmaline-granite with a few areas of biotite granite (Wolfaardt 2000) (Figure 1.3). The granites found in the interior of the island have weathered into flat exfoliated masses, some of which form temporary pans in winter. The granites found along the coast, to just above the high-water mark, consist of large, rounded boulders. The central part of the island is covered primarily with coarse, shell-derived sediments (Figure 1.3), with small areas covered by recent limestone sediments.

The geology of the island has an important influence on the nesting habitats available for African Penguins. The majority of penguins (>90%) breed under cover in burrows that are dug into the sandy substrate, in among granite boulders or under shrubs; the remainder nest in the open (unpubl. data).

Dassen Island experiences a temperate, Mediterranean-type climate, with warm, dry summer and cool, relatively wet, winter seasons. The rainfall occurs as a result of cold fronts moving in from the south Atlantic Ocean. From 1990–2005, the island received an average annual rainfall of 336 mm (SD = 66 mm). Most of the rain occurs from April until September, normally peaking in June, although there is some inter-annual variation in the timing of this peak (Figure 1.4). The warmest mean monthly temperatures are recorded from December until March; the coldest month is July (Figure 1.5). The cold Atlantic Ocean has a tempering effect on temperatures. Both rainfall and ambient temperature are known to impact the breeding success of African Penguins. Burrows are prone to collapse and flooding in heavy rain, and penguins often desert their nests during periods of increased ambient temperature, especially if they are breeding in open nests (Frost *et al.* 1976b, Crawford *et al.* 1986, Randall *et al.* 1986, La Cock 1988, Seddon & van Heezik 1991, Murison 1998).

There is a long history of human activity on the island. Jan van Riebeeck ordered the first settlement of Dassen Island in 1654 to prevent intruders from gaining access to the island (Green 1946). The island was used to provide ships with the products of penguins and other marine life. Although penguins were killed for food, for fuel to supply the boilers of ships, and for fat, the main attraction was their eggs. Not much is known about the quantities of eggs collected prior to the 1900s. Harvests of eggs at Dassen Island were high in the early 1900s, with close to 600 000 eggs being collected in 1919 alone (Randall 1989). A penguin exclusion wall was built around the outer perimeter of the island (see Figure 1.3) in the early 1940s to facilitate egg collecting (Rand 1960). The commercial harvesting of eggs at Dassen Island was terminated in 1967 (Shelton *et al.* 1984).

Commercial guano-scraping activities were initiated at Dassen Island in the early 1840s (Skead 1999). Guano, a Peruvian Indian word for seabird manure, was harvested for use as an agricultural fertilizer, rich in nitrogen. At Dassen Island the guano was mostly

obtained from Cape Cormorants, *Phalacrocorax capensis*. Penguin guano at Dassen Island was not as suitable for commercial harvesting because of the sandy nature of the substrate on which the penguins nest, and in which the guano becomes dissipated (Brooke & Crowe 1982). Phosphatic sand was also removed from Dassen Island to replace nesting material at gannet colonies on other islands where guano had been removed (Ross & Randall 1990). The scraping of guano on the island for commercial purposes was discontinued in 1974 (Siegfried & Crawford 1978).

A lighthouse was established on the island in 1893, and has been manned ever since. The lighthouse and associated buildings are located on the southern side of the island (Figure 1.3).

As a result of human activity a number of alien plants and a lesser number of alien animals have become established at Dassen Island (Cooper *et al.* 1985, Brooke & Prins 1986). Of greatest impact to the African Penguin was the Feral Cat *Felis catus*, which preyed on the chicks of African Penguins and other seabirds (Wolfaardt 2000). It is not known exactly when domestic cats were first introduced, but it was probably towards the end of the 19th Century, to control the population of House Mice *Mus musculus* (Cooper *et al.* 1985). Feral Cat numbers were controlled intermittently until 1979 when a study of the cat population on the island was initiated (Apps 1983). Apps (1983) suggested that the adverse effects of Feral Cats on the avifauna of Dassen Island were not serious enough to necessitate their control. However, on the basis of a separate research project conducted at Dassen Island (Berruti 1986), and the fact that Feral Cats have been responsible for the extinction of at least 33 bird species, most of which bred on islands (Lever 1994, Nogales *et al.* 2004), most researchers studying aspects of seabird ecology and conservation in South Africa strongly disagreed (e.g. Cooper *et al.* 1985, Berruti 1986, Crawford *et al.* 1995b, Whittington *et al.* 2000). Consequently, a Feral Cat eradication programme was initiated in 1995 (Wolfaardt 2000). The initial implementation of the programme was of an opportunistic nature. Feral Cats were finally eradicated from Dassen Island in 2002.

From the 1860s Dassen Island has been controlled by a succession of government organisations. The island was ceded to the Chief Directorate Nature and Environmental Conservation in 1987 and was gazetted as a Provincial Nature Reserve on the 18th of

March 1988 (Government Gazette, 18 March 1988, No. 12/1988). It is presently managed by the Western Cape Nature Conservation Board (or CapeNature), and is protected primarily for the seabird and shorebird species that breed and roost on the island (Appendix 1.1). Seabird species and colonies are currently protected in South Africa by the Sea Birds and Seals Protection Act (No. 46 of 1973). The African Penguin is further listed as a "Protected Species" in South Africa's National Environmental Management: Biodiversity Act (No. 10 of 2004).

BACKGROUND TO THIS STUDY

At the time this study was initiated in 1994, little was known about the efficacy and conservation value of de-oiling African Penguins. Some opportunistic re-sighting work in the 1970s and early 1980s suggested that de-oiling African Penguins could be justified on conservation grounds (Randall *et al.* 1980, Morant *et al.* 1981), but this work was of a short-term nature. Moreover, the interpretation of the results as justifying the conservation value of de-oiling contaminated African Penguins was questioned by other researchers (Fry & Lowenstine 1985, Fry *et al.* 1986, Nisbet 1994, Boersma 1995). The main concern expressed by these authors was the relatively low proportion of de-oiled birds that had been recorded breeding subsequent to their release.

The sinking of the *Apollo Sea*, a bulk iron-ore carrier near Dassen Island in June 1994 (Erasmus 1995) provided an opportunity to determine the population benefits and conservation value of de-oiling African Penguins. This information was considered vital by the conservation authorities to inform policy and action plans on how to prepare for and respond to future oil spill events (Barrett *et al.* 1995). Six years later, another iron-ore carrier, the *Treasure*, sank between Robben and Dassen Islands, spilling approximately 1 400 tonnes of oil (Cheney 2000, Crawford *et al.* 2000b). From an operational perspective, the authorities were able to implement lessons learnt from the *Apollo Sea* spill. The *Treasure* spill also provided an opportunity to broaden our understanding of the impacts of oil spills on African Penguins, including the population level benefits of de-oiling contaminated birds.

This is the second of two PhD projects that have analysed two key questions relating to de-oiled African Penguins: (1) Do they survive as well as never-oiled penguins? (2) Do they go on to breed as well as never-oiled penguins? The PhD thesis of Dr Phil Whittington (2002) answered the first question. This PhD answers the second.

STRUCTURE AND OUTLINE OF THESIS

Each chapter of this thesis has been written as an independent paper to facilitate publication of the results. This has resulted in some overlap in the introductory sections of each chapter. References have been included within the separate chapters, rather than as a composite list at the end of the thesis.

The precise definition of key terms has an important bearing on how the objectives of a research project are formulated and measured, and also influences the understanding and uptake of the research findings by other researchers and practitioners. "Rehabilitation" and "restoration" are terms which have been variously applied in the literature in relation to the oiling and subsequent cleaning and release of seabirds and other fauna, as well as more broadly (e.g. Hobbs & Norton 1996, Grenfell *et al.* 2007). In this thesis, I have restricted the expression "rehabilitated" to birds that have been de-oiled (by which I mean cleaned of oil and subsequently released) and which survive in the wild for a further month or more. The term "restored" is used for de-oiled birds, which subsequently have been found breeding in the wild.

Chapter Two examines the extent to which de-oiled African Penguins from the *Apollo Sea* spill were successfully restored into the breeding population at Dassen Island over a period of 10.5 years. It also investigates whether there is a cost of reproduction for those individuals that were able to breed following release.

Chapters Three and Four focus on the moult and breeding phenology of African Penguins at Dassen and Robben Islands. Chapter Three examines the annual cycle of African Penguins at Dassen Island in order to assess if and how the *Apollo Sea* and *Treasure* oil spills disrupted the timing and synchrony of breeding and moult cycles. Chapter Four compares the patterns of moult of adult and juvenile African Penguins at

Dassen and Robben Islands, which are approximately 50km apart, and assesses the efficacy of moult counts as population monitoring tools.

Chapter Five analyses the breeding success of de-oiled birds from the *Apollo Sea* spill over a period of five and a half years, including the growth rates of chicks raised by de-oiled parents. This is compared with the breeding success of never-oiled birds to quantify the impact of oiling on the productivity of de-oiled birds. The influence of oiling on the average rates of mate fidelity for African Penguins, and how this may influence their reproductive success, is also investigated.

Chapter Six is presented as a case study of the seabird rescue operation that followed the *Treasure* oil spill in June 2000. The success of the operation is compared with that which followed the *Apollo Sea* spill, six years before. The rehabilitation and restoration success of the rescue and treatment process is assessed for three groups of birds: 1) de-oiled penguins; 2) un-oiled birds that were evacuated during the spill and 3) orphaned chicks that were hand-reared following the spill. The overall impact of the *Treasure* oil spill on the breeding population in the five years following the spill is also examined.

Chapter Seven provides a review of the rescue, rehabilitation and restoration of oiled seabirds in South Africa, mostly focussing on African Penguins and Cape Gannets. It incorporates the findings of other chapters in this thesis, as well as from previous and recent research in the field.

Finally, in the Conclusions and synthesis chapter (Chapter Eight), I attempt to integrate the findings of the separate chapters to provide an overview of the work as a whole. Suggestions for future research are also provided.

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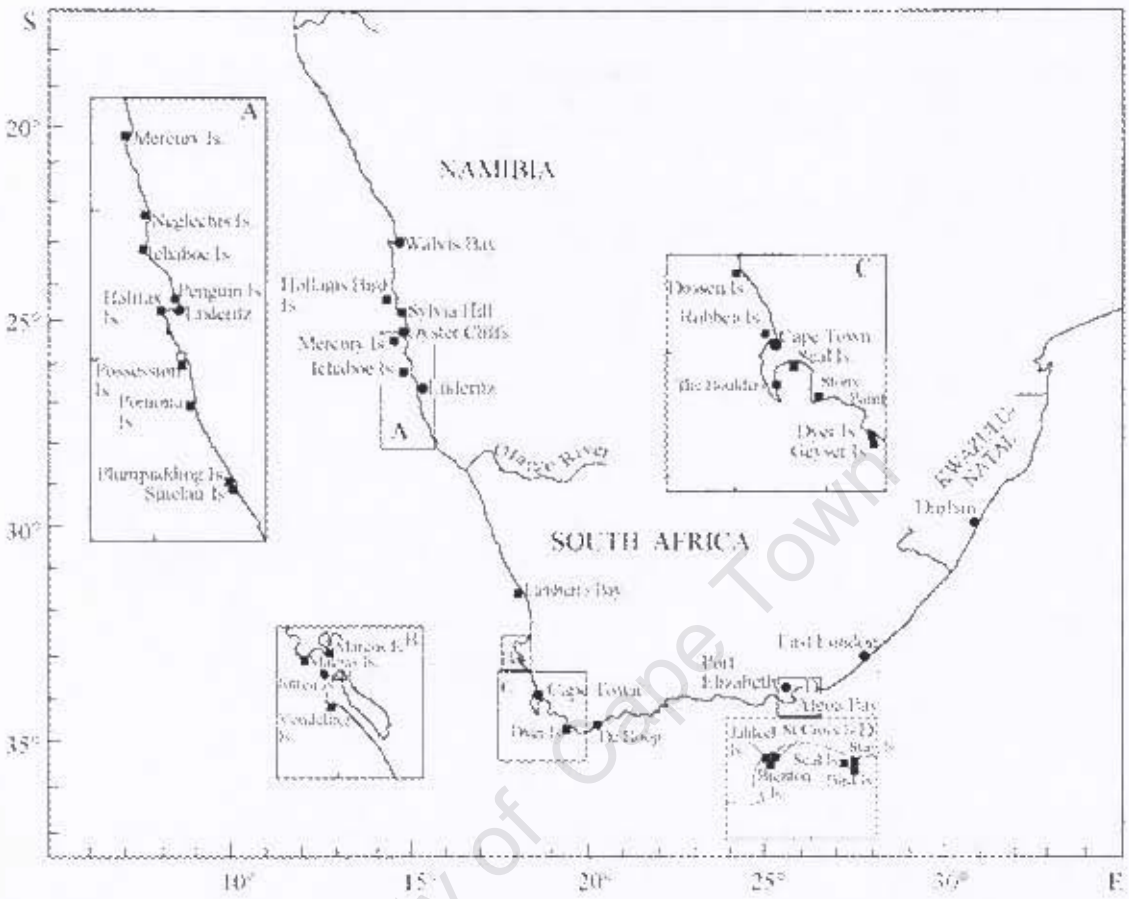

Figure 1.1 The locations of the 32 breeding colonies of African Penguins, which were extant at some stage during the period 1978–2006. The three broad regions of the breeding range include Namibia (A), the Western Cape (A-C, and Lambert's Bay and De Hoop) and the Eastern Cape (D). Adapted from Crawford *et al.* (2007).

Figure 1.3 Map of Dassen Island Nature Reserve showing the geology of the island, as well as the layout of the main infrastructure. Adapted from Wolfaardt (2000).

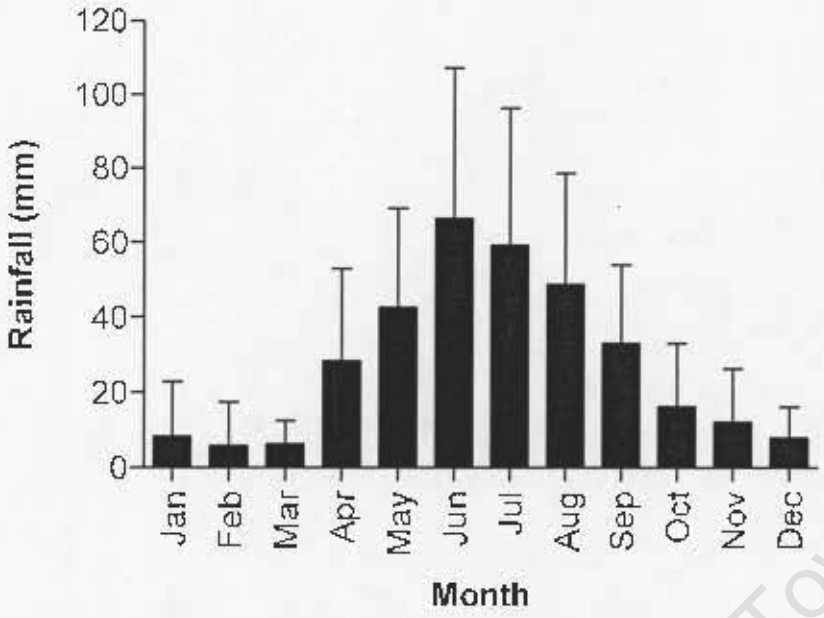

Figure 1.4 Mean monthly rainfall recorded at Dassen Island between 1990 and 2005. The error bars denote one standard deviation (data provided by the South African Weather Service).

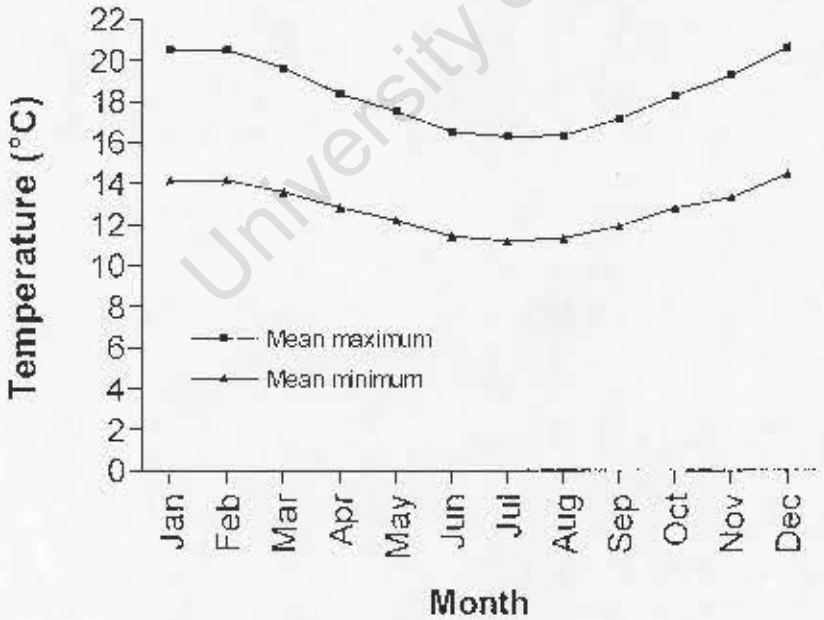

Figure 1.5 Mean monthly maximum and minimum temperatures recorded at Dassen Island between 1990 and 2005 (data provided by the South African Weather Service).

Appendix 1.1 Checklist of birds recorded at Dassen Island Nature Reserve. Species which breed on the island have been denoted as BR in the Population Status column; those which are found regularly on the island but which have not been recorded breeding are denoted NBR. Vagrants refer to species outside their normal range and whose presence at Dassen Island is assumed to be aberrant (from Wolfaardt 2000).

Scientific Name	Common Name	Details of sightings	Population Status
Spheniscus demersus	African Penguin	Throughout the year	BR
Diomeda cauta	Shy Albatross	Offshore	Rare
Diomedea melanophris	Black-browed Albatross	Offshore	Uncommon
Diomeda chlorohynchos	Yellow-nosed Albatross	Offshore	Vagrant
Phoebetria palbebrata	Light-mantled Sooty Albatross	Offshore	Vagrant
Macronectes giganteus	Southern Giant Petrel	Offshore	Uncommon
Daption capense	Pintado Petrel	Offshore	Vagrant
Pterodroma mollis	Softplumaged Petrel	Offshore	Vagrant
Pachyptila belcheri	Slender-billed Prion	Found dead on island, 18/7/1999	Vagrant
Procellaria aequinoctialis	White-chinned Petrel	Offshore	Mostly winter visitor, NBR
Calonectris diomedea	Cory's Shearwater	Found dead on island 2/4/2000	Vagrant
Puffinus gravis	Great Shearwater	Offshore	Rare, passage migrant
Puffinus griseus	Sooty Shearwater	Offshore	Mostly winter visitor, NBR
Oceanodroma leucorhoa	Leach's Storm Petrel	Since November 1996	BR
Oceanites oceanicus	Wilson's Storm Petrel	Offshore	Occasional, NBR
Pelecanus onocrotalus	White Pelican	August to March	BR
Morus capensis	Cape Gannet	Offshore	Common, NBR
Phalacrocorax carbo	White-breasted Cormorant	Throughout the year	BR
Phalacrocorax capensis	Cape Cormorant	Throughout the year	BR
Phalacrocorax neglectus	Bank Cormorant	Throughout the year	BR
Phalacrocorax coronatus	Crowned Cormorant	Throughout the year	BR
Ardea cinerea	Grey Heron	Uncommon	Occasional visitor
Ardea melanocephalus	Blackheaded Heron	Mostly in summer	NBR visitor
Egretta garzetta	Little Egret	Throughout the year	NBR
Bubulcus ibis	Cattle Egret		Vagrant
Nycticorax nycticorax	Black-crowned Night Heron	Throughout the year	NBR
Ciconia ciconia	White Stork		Vagrant
Threskiornis aethiopicus	Sacred Ibis	Throughout the year	BR
Plegadis falcinellus	Glossy Ibis		Vagrant
Alopochen aegypticus	Egyptian Goose	Throughout the year	BR
Tadorna cana	South African Shelduck	Mostly in winter	Winter visitor, observed breeding October 1999
Anas undulata	Yellow-billed Duck		Vagrant
Anas capensis	Cape Teal		Vagrant

Scientific Name	Common Name	Details of sightings	Population Status
Plectopterus gambensis	Spurwing Goose		Vagrant
Milvus migrans	Yellowbilled Kite	October 1996	Vagrant
Elanus caeruleus	Black shouldered Kite		Uncommon visitor
Gypohierax angolensis	Palmnut Vulture	October 1997	Vagrant
Buteo buteo	Steppe Buzzard		Vagrant
Accipiter sp.	Unidentified Goshawk		Vagrant
Falco peregrinus	Peregrine Falcon	Hunting waders, March 1996	Vagrant
Falco tinnunculus	Rock Kestrel		Uncommon visitor
Francolinus capensis	Cape Francolin		Vagrant
Coturnix coturnix	Common Quail	December 1998	Vagrant
Numida meleagris	Helmeted Guinea Fowl	Throughout the year	Introduced, BR
Porphyrula martinica	American Purple Gallinule	May 1996 & June 2000, both died	Vagrant
Fulica cristata	Redknobbed Coot		Vagrant
Haematopus ostralegus	European Oystercatcher		Vagrant
Haematopus moquini	African Black Oystercatcher	Throughout the year	BR
Charadrius hiaticula	Ringed Plover		Summer visitor, NBR
Charadrius marginatus	White-fronted Plover		BR
Charadrius pecuarius	Kittlitz's Plover		BR
Charadrius tricollaris	Threebanded Plover		Uncommon summer visitor, NBR
Pluvialis dominca	American Golden Plover		Vagrant
Pluvialis squatorola	Grey Plover		Summer visitor, NBR
Vanellus coronatus	Crowned Plover		BR
Vanellus armatus	Blacksmith Plover	Throughout the year	BR
Areneria interpres	Turnstone	Most abundant in summer	NBR
Actitus hypoleucos	Common Sandpiper		Vagrant
Tringa nebularia	Greenshank		Vagrant
Calidris canutus	Knot	October 1996	Vagrant
Calidris ferruginea	Curlew Sandpiper		Summer visitor, NBR
Calidris minuta	Little Stint		Uncommon summer visitor, NBR
Calidris alba	Sanderling		NBR visitor, mainly summer
Limosa lapponica	Bartailed Godwit	October-November 1996	Vagrant
Numenius arquata	Curlew		Vagrant
Numenius phaeopus	Whimbrel		Vagrant
Himantopus himantopus	Blackwinged Stilt		Vagrant
Burhinus capensis	Spotted Dikkop		Vagrant
Stercorarius parasiticus	Arctic Skua	Offshore	Summer visitor, NBR
Catharacta antarctica	Subantarctic Skua	Offshore	Winter visitor, NBR
Larus dominicanus	Kelp Gull	Throughout the year	BR
Larus hartlaubii	Hartlaub's Gull	Throughout the year	BR
Larus sabini	Sabine's Gull	Offshore	Summer visitor, sometimes numerous, NBR
Sterna bergii	Swift Tern	Throughout the year	BR
Sterna sandvicensis	Sandwich Tern		Summer visitor, NBR
Sterna hirundo	Common Tern		Summer visitor, NBR

Scientific Name	Common Name	Details of sightings	Population Status
Sterna paradisaea	Arctic Tern	Offshore	Vagrant
Sterna vittata	Antarctic Tern		Winter visitor, NBR
Chlodonias niger	Black Tern		Vagrant
Columba livia	Feral Pigeon		Vagrant
Columba guinea	Rock Pigeon	Throughout the year	BR
Streptopelia senegalensis	Laughing Dove		Vagrant
Oena capensis	Namaqua Dove		Vagrant
Tyto alba	Barn Owl		Vagrant
Apus barbatus	Black Swift		Vagrant
Apus caffer	White-rumped Swift	Around houses, October 1999	Rare
Apus affinis	Little Swift		Rare
Eremopterix verticalis	Grey-backed Finchlark	January 1996	Vagrant
Hirundo rustica	European Swallow		Rare summer visitor
Hirundo fuligula	Rock Martin		Vagrant
Riparia paludicola	Brownthroated Martin		Vagrant
Riparia cincta	Banded Martin		Vagrant
Psalidoprocne holomelas	Black saw-wing swallow	October 1996	Vagrant
Corvus albus	Pied Crow		Rare visitor, has bred on island (BR)
Turdus olivaceus	Olive Thrush		Vagrant
Oenanthe pileata	Capped Wheatear	May 1995	Vagrant
Parisoma layardi	Layard's Titbabbler	Dead bird found in May 1997	Vagrant
Acrocephalus baeticatus	African Marsh Warbler	October 1998	Vagrant
Bradypterus baboecala	African Sedge Warbler		Vagrant
Phylloscopus trochilus	Willow Warbler		Vagrant
Terpsiphone viridis	Paradise Flycatcher		Vagrant
Motacilla capensis	Cape Wagtail	Throughout the year	BR
Lanius collaris	Fiscal Shrike		Vagrant
Sturnus vulgaris	European Starling	Throughout the year	BR
Creatophora cinerea	Wattled Starling		Vagrant
Nectarinia famosa	Malachite Sunbird		Vagrant
Nectarinia chalybea	Lesser Double-collared Sunbird		Vagrant
Zosterops pallidus	Cape White-eye		Vagrant
Passer domesticus	House Sparrow	Throughout the year	BR
Passer melanurus	Cape Sparrow		Vagrant
Serinus canicollis	Cape Canary	December 1999, Boom Point	Vagrant
Emberiza tahapisi	Rock Bunting	May 1999	Vagrant
Chionis alba	Greater Sheathbill		Vagrant
Anus platyrhynchos	Mallard Duck		Vagrant
	Diamond Firetail		Escaped pet
	Muscovie Duck	Removed 12 April 1994	Captive pets previously kept on island
	Bantam Chicken	Removed 12 April 1994	Captive fowl previously kept on island
	Domestic Chicken	Removed 12 April 1994	Captive fowl previously kept on island
	Domestic Goose	Removed 12 April 1994	Captive fowl previously kept on island
	Turkey	Removed 12 April 1994	Captive fowl previously kept on island

Chapter Two

Proportion of rehabilitated African Penguins *Spheniscus demersus* attempting to breed following the *Apollo Sea* oil spill

Proportion of rehabilitated African Penguins *Spheniscus demersus* attempting to breed following the *Apollo Sea* oil spill

ABSTRACT

The bulk ore carrier *Apollo Sea* sank southwest of Dassen Island in June 1994, oiling approximately 10 000 African Penguins *Spheniscus demersus*, most of which were collected from Dassen Island. A total of 4 076 de-oiled penguins were released with flipper bands. From 1994–2005 follow-up research using re-sighting and capture-mark-recapture methods indicated that about 74% of the de-oiled penguins observed back at Dassen Island attempted to breed, and were thus successfully restored into the breeding population. For de-oiled breeders, the median interval between their first recorded sighting and first recorded breeding attempt was 11 months, indicating a short-term delay in restoration. At least 45% of the de-oiled breeders were still being re-sighted five years after their release, and a minimum of 4% survived into their ninth year. These results represent the most successful restoration estimates anywhere in the world. The proportion of de-oiled juvenile penguins re-sighted back at Dassen Island and recorded breeding was lower than that of birds in adult plumage. De-oiled nonbreeders spent significantly more time along the shore and less time within breeding colonies than de-oiled breeders. The mean proportion of de-oiled breeders which abstained from breeding each year during the study period was greater than expected. There was a negative relationship between breeding and subsequent survival and breeding, suggesting a cost of reproduction for de-oiled birds.

INTRODUCTION

The coastal waters of South Africa, and especially the southwestern coasts, are a global hotspot for oil pollution (Moldan & Dehrmann 1989, Nel & Whittington 2003). The African Penguin *Spheniscus demersus*, classified as Vulnerable due to its continued population decline (Crawford 2000, Whittington *et al.* 2000, du Toit *et al.* 2003, BirdLife International 2004), is one of the species most threatened by oil pollution in southern Africa. The rate of oiling has increased markedly over the last few decades (Adams 1994, Whittington 2002, Chapter Seven); 77% of all penguins oiled between 1968 and 2002 were recorded between 1991 and 2000 (Nel *et al.* 2003), mostly as a result of two large oil spills, the *Apollo Sea* in June 1994 (Underhill *et al.* 1999) and the *Treasure* in 2000 (Crawford *et al.*

2000). Currently oil pollution is considered to be one of the main threats to the African Penguin (Whittington *et al.* 2000, Nel *et al.* 2003).

The closure of the Suez Canal in 1967 and the diversion of oil tankers around southern Africa resulted in increased contamination of seabirds, especially African Penguins (Westphal & Rowan 1969). A large oil spill near Cape Town in 1968 led to the establishment of the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), whose primary aim was to clean and rehabilitate oiled seabirds (Westphal & Rowan 1969, Morant *et al.* 1981, Moldan & Westphal 1989, 1994). The biological and conservation value of rehabilitation as a wildlife management intervention has been questioned (e.g. Estes 1991, Boersma 1995, Anderson *et al.* 1996, Sharp 1996) including by Frost *et al.* (1976) for African Penguins. The design of a stainless steel flipper band for the African Penguin (Jarvis 1970, Cooper & Morant 1981) has made it possible to test the effectiveness of cleaning efforts. Subsequent post-release studies have shown that, in contrast to rehabilitation activities elsewhere (e.g. Khan & Ryan 1991, Sharp 1996, Wernham *et al.* 1997), de-oiled African Penguins have a high survival rate (Randall *et al.* 1980, Morant *et al.* 1981), similar to that of non-oiled birds (Underhill *et al.* 1999, Whittington 1999a, 2002). Evidence from these studies suggests that rehabilitation of oiled African Penguins makes an important contribution to the conservation of this species.

However, in conservation terms, rehabilitation is of little value unless these birds breed again. The overall success of the rehabilitation process should therefore also take into account the reproductive output of birds after release. If rehabilitated birds survive for months or years, but never produce offspring, they are effectively redundant to the population. It can even be argued that rehabilitated birds that never produce offspring actually have a potentially negative impact on the breeding population by competing for scarce resources. In this study, a rehabilitated bird is one which has been de-oiled (cleaned, treated and subsequently released), and that has survived in the wild for at least one month. The term restored is used for rehabilitated birds that have been found breeding in the wild (Underhill *et al.* 1999).

Randall *et al.* (1980) followed the fortunes of 150 African Penguins oiled at St Croix Island, South Africa over a six month period. Of the 106 birds that were released, 80

were re-sighted at the island, and six were recorded breeding there. Morant *et al.* (1981) reported that 20% of the rehabilitated birds seen back at colonies after seven major oiling incidents, including the St Croix spill, had been recorded breeding. Unfortunately Morant *et al.* (1981) did not indicate the degree of search effort nor the period over which re-sightings were attempted. The main objective of these early studies was to establish that some de-oiled penguins did breed, but they were not sufficiently intensive to estimate whether all de-oiled penguins breed again, or if there was a proportion which does not breed. Giese *et al.* (2000) and Goldsworthy *et al.* (2000) studied the post-release survival and breeding success of rehabilitated oiled Little Penguins *Eudyptula minor* over a two year period, but did not report the proportion of oiled rehabilitated birds attempting to breed.

The bulk ore carrier *Apollo Sea* sank southwest of Dassen Island (33°25'S, 18°05'E) at approximately 33°32'S, 17°50'E in June 1994 (Erasmus 1995). Heavy fuel oil washed ashore at both Dassen and Robben (33°48'S, 18°23'E) Islands, contaminating about 10 000 penguins (Dehrmann 1994a). About 7 200 of these were caught at Dassen Island and 2 400 at Robben Island; the remainder were caught at other island colonies and on the mainland coastline (Crawford 1994, Dehrmann 1994a, Crawford 1995). Approximately 4 800 (48%) of the oiled penguins were successfully released after de-oiling; of the 52% which died, about half of the deaths occurred in the first 48 hours after collection (Williams 1995a).

This study documents the systematic follow-up of de-oiled African Penguins after the *Apollo Sea* oil spill over a period of 10.5 years, from September 1994 up until March 2005, to assess the restoration success of cleaning oiled African Penguins. Previous studies focused mostly on the post-release survival, and rehabilitation success, of the oil spill victims over a three to five year period (Underhill *et al.* 1997, 1999, 2000, Whittington 2002). The aim of this study is to examine the extent to which de-oiled African Penguins are successfully restored into the breeding population, thereby allowing a better assessment of the conservation value of cleaning oiled birds for this species.

STUDY AREA AND METHODS

Dassen Island is located approximately 55km north west of Cape Town (Figure 2.1). It is a classified "Important Bird Area" (Barnes 1998), and supported the worlds' largest African Penguin colony during the period of the study (du Toit *et al.* 2004). The majority of penguins (over 90%) breed under cover in burrows, in among granite boulders or under shrubs; the remainder nest in the open (unpubl. data). The island is divided into nine monitoring areas and management areas, Areas A–I (Figure 2.2).

A total of 4 076 de-oiled penguins were released with flipper bands, most at Silwerstroomstrand (33°34'S, 18°21'E), a mainland beach between Dassen and Robben Islands (Underhill *et al.* 1999). This total comprised 3 488 birds in adult plumage and 348 in juvenile plumage, henceforth referred to as *Apollo Sea* adults and juveniles, respectively. An additional 240 flipper-banded birds that were released did not have their age recorded on the banding schedules. Based on results in Whittington (2002) it is likely that the majority of these birds were adults, and they will be treated as such in this study. All birds were released between 26 July and 11 September 1994 (Underhill *et al.* 1999). It is not known what proportion of the birds that survived the cleaning process and were ultimately released originally came from Dassen and Robben Islands. Unfortunately, c. 700 de-oiled birds were released without flipper bands, and these are therefore indistinguishable from birds which have never been oiled.

Systematic searches for flipper-banded penguins began at Dassen Island in September 1994, one month after most of the penguins had been released; this chapter reports results until March 2005. Each flipper band has a unique number and can be read from a distance of up to 50m with a spotting scope. During weekly coastal surveys, binoculars and a spotting scope were used to search for flipper-banded penguins along the shore. All nest sites were examined and flipper-bands recorded during surveys of two breeding study colonies set up as part of this study, Area G and Area B (Figure 2.2). These were the colonies on Dassen Island where the largest numbers of oiled penguins had been caught (A.J. Williams pers. comm.), and hence where the most intensive monitoring took place. Until the end of 1995 surveys were monthly; thereafter they took place twice a month. Surveys of all nest sites in two smaller study areas (within Areas F and D) were also conducted, monthly until the end of 1995, and then twice monthly. An additional

study area was set up in Area A in May 1997, which was surveyed fortnightly until the end of the study period. A penguin census of the entire island was conducted annually, between April and June of each year. During these censuses, all active nests were examined for flipper-banded penguins. Opportunistic re-sightings of flipper-banded birds during the course of the study period were also recorded. The activity of the bird for each re-sighting was recorded (Table 2.1). A bird was regarded as breeding if it was observed incubating eggs or brooding or guarding chicks. The management area (A–I), the locality (whether the bird was observed on the beach or in a breeding colony), as well as the nest type (where relevant) were also recorded for each re-sighting. All re-sighting data were incorporated into a database for further analysis. Data from the South African Bird Ringing Unit, SAFRING, relating to African Penguins flipper-banded, re-sighted and recovered dead at other localities were incorporated into the Dassen Island database because some birds are known to move between different colonies (Whittington *et al.* 2005b). The Dassen Island data are curated within the SAFRING database. The number of oil spill survivors and the proportion of those released that were recorded breeding were investigated for two age classes of birds: birds released in adult plumage (n=3 728) and those released as juveniles (n=348).

I compared whether there was a tendency for de-oiled birds that were never recorded breeding to be seen less frequently in a breeding colony as opposed to on the beach. For each bird, I recorded the number of re-sightings in the colony and the number of re-sightings on the beach. These were used as explanatory variables in a logistic regression with the response variable being whether the bird had been recorded breeding (response = 1) or not (response = 0). Due to the low number of un-oiled penguins that were flipper-banded, and a temporary moratorium on flipper banding at the time the study was initiated, I was unable to include an un-oiled control group in this analysis.

Capture-Mark-Recapture (CMR) analyses

Multi-state capture-mark-recapture (CMR) models were used to estimate the probability of adult penguins attempting to breed after having been de-oiled, and to estimate the survival of birds in each state. In the model, penguins assumed one of three different reproductive states each year: non-breeder (n), breeder (b) and secondary nonbreeder (s) (Figure 2.3). Nonbreeders were defined as birds that were observed at least once in

the current year, but not recorded breeding; breeders as birds that were observed incubating eggs, brooding or guarding chicks (i.e. breeding) during the current year; and secondary nonbreeders as birds that were observed but did not reproduce during the current year, but had been recorded breeding previously (post de-oiling). The reason for including a secondary nonbreeder state was to examine possible costs of breeding for birds that were de-oiled. Furthermore, these birds were suspected to have different recapture probabilities to those in other states. CMR models allow a distinction to be made between survival and the recapture probability (the probability of being recaptured at a certain occasion given that the individual was alive) (Lebreton *et al.* 1992, Nichols *et al.* 1994). The design is based on the approach outlined in (McElligott *et al.* 2002).

A capture history matrix was constructed for each adult *Apollo Sea* survivor that was seen back at Dassen Island, and also included observations of these birds at other colonies. Recapture periods were not calendar years, but were set to start in March and end in February of the following year, except for 1994, which started in September 1994 (the beginning of the study) and ended in February 1995. The February to March recapture period was set to coincide with the end of the peak moult period (February) for penguins at Dassen Island (Chapter Three).

I first examined the survival and breeding of all adult de-oiled birds subsequently observed on Dassen Island. For this analysis, the initial sighting for an individual was taken to be the first sighting on Dassen Island, either as a nonbreeder or a breeder. The data were suspected to contain transients, especially among nonbreeders. Because it was not possible to distinguish between permanent emigration and survival, transients would have resulted in survival being underestimated during the interval after the initial sighting. This transient effect was accounted for by allowing survival to be lower during those intervals (Pradel *et al.* 1997). Re-sightings of banded penguins were made in all areas of the island, but most intensively in Area G and Area B. The CMR analysis was restricted to these two study areas. Preliminary analyses showed no evidence for differences between the areas in any of the parameters, and the data were thus pooled. The capture history of the de-oiled birds re-sighted at Dassen Island also included observations of these birds at other colonies, which were obtained from the SAFRING database.

The most general model included a transients effect, independent time effects on survival and recapture in all three stages, and time dependence in the three possible transition rates (Model 12, Table 2.2). The goodness of fit for this model was assessed using the median *c*-hat approach in the program MARK (White & Burnham 1999). With five replicate simulations at 10 levels of overdispersion, this test showed that the overdispersion in the data was small (estimated *c*-hat = 1.087), and that the model was therefore a good starting point for model selection. All other models were simplified versions of this general model. The relative performance of all models was assessed using Akaike's Information Criterion, adjusted for sample size (AICc). The best model is the one with the lowest AICc value (Burnham & Anderson 2002). All models were fitted using program MARK 4.3 (White & Burnham 1999). Parameter estimates and confidence intervals are reported from Model 2, which differed only marginally from Model 1 in its AICc, and was more parsimonious (Table 2.2).

The main objective of the CMR analyses was to determine whether there were differences in survival between birds in each stage, and the probability of changing between different states. The above analyses provided these estimates for those birds that arrived back at Dassen Island. However, an additional objective of the study was to determine how long it took for the de-oiled penguins to start breeding after they had been released from the rehabilitation centre. Therefore, banding at the rehabilitation centre (SANCCOB) was included as the first observation for each individual, at which point all birds were classified as non-breeders. For this analysis, only individuals that were later encountered at Dassen Island were included; it does not therefore provide estimates of breeding probabilities for all de-oiled penguins. Rather, the surviving part of the Dassen Island population is examined to determine when they started breeding again after having been de-oiled and released.

RESULTS

Re-sightings

Between September 1994 and March 2005, 57 451 re-sightings of flipper-banded African Penguins were made at Dassen Island. These re-sightings involved 10 477 individual birds, 2 499 of which were *Apollo Sea* survivors. Of the 2 499 *Apollo Sea*

survivors re-sighted, 2 444 were birds that were released in adult plumage (65% of those released in adult plumage), and 55 were birds released in juvenile plumage (16% of those released in juvenile plumage). The 55 juvenile penguins re-sighted did not represent the total number of de-oiled juveniles re-sighted, only those observed at Dassen Island; an additional 50 juveniles had been re-sighted at other colonies by 1999 (Whittington 2002). Nine penguins were found dead during their first post-release moult as a result of gangrene poisoning caused by the flipper bands having been fitted too tightly (Underhill 1995). The tight bands did not allow sufficient space for the expansion of the flipper during moult. This caused wounds to develop, that subsequently became gangrenous. Consequently, searches were made for other penguins with flipper bands that had been fitted too tightly. As a precaution, a total of 69 ill-fitted flipper bands were removed from penguins on Dassen Island, which were then released without bands. These birds were excluded from all further analyses. The numbers and proportions of *Apollo Sea* survivors reported here represent only those birds sighted at Dassen Island, and do not reflect the total number sighted after release. Re-sighting information for birds that were observed at Dassen Island and also at other colonies is included. Ten percent (n=240) of the adult *Apollo Sea* birds re-sighted at Dassen Island were also observed at other colonies. Re-sightings of these birds at colonies other than Dassen Island amounted to an additional 577 observations.

Birds recorded breeding

By March 2005, 1 459 (61%) of the de-oiled adult birds that had been re-sighted at Dassen Island had been recorded breeding (Figure 2.4); the proportion increased to 70% and 74% when the analysis was restricted to birds observed in Areas G and B, respectively (Table 2.3). The majority of these birds (97%) were recorded breeding at Dassen Island. Of 45 birds observed at least once at Dassen Island and recorded breeding elsewhere, 43 were recorded breeding at Robben Island, and two at Jutten Island (33°05'S, 17°58'E) (Figure 2.1). The number of de-oiled birds which were recorded breeding at Dassen Island, and which were also observed (not breeding) at other colonies was 106; Robben Island was the colony visited on the majority (85%) of these occasions. The pattern of cumulative re-sightings of de-oiled birds over time was similar for the island as a whole and for Areas G and B, in terms of both the birds re-sighted and birds recorded breeding (Figure 2.5). In all three cases, the cumulative figures became almost stable by the end of 1997, approximately 30 months after the

birds were released. However, small numbers of previously unrecorded birds continued to be re-sighted and recorded breeding for the first time up until June 2004. The long time series shown in Figure 2.5 masks the step-wise pattern in the rate of restoration, especially in the first two years following release (Figure 2.6). Twenty-two of the re-sighted juveniles (40% of those re-sighted at Dassen Island) had been recorded breeding by March 2005. All but two of these birds bred at Dassen Island. The other recorded breeding was at Robben and Jutten Islands.

Of the adult birds recorded breeding during the study, over 70% were first re-sighted as breeders by the end of 1996, within 28 months of their release (Figure 2.7). The time that elapsed between release and when the birds were first detected breeding ranged from less than a month to 115 months. The median time elapsed between release and first recorded breeding was 15 months. The median interval between when the bird was first observed at Dassen Island and when it was first recorded breeding (excluding birds that were observed breeding on the first occasion they were re-sighted) was 11.3 months (the five number summary (minimum, lower quartile, median, upper quartile, maximum) was 0.07, 4.2, 11.3, 24.9, 108). At least 655 of the penguins recorded as breeders (27% of those re-sighted at Dassen, and 45% of those recorded breeding) were known to have survived into their fifth year following release from SANCCOB; 64 *Apollo Sea* breeders survived into their ninth year (Figure 2.4). The number of years in which *Apollo Sea* breeders were recorded breeding ranged from one to 10. Thirty-six of these birds (2.5% of the total number of de-oiled *Apollo Sea* adults that were recorded breeding) were observed breeding in more than eight of the 10 years of the study (Table 2.4).

The proportion of re-sighted birds that were recorded breeding each year increased steadily from 36% in 1994 (i.e. 36% of the birds observed in 1994 were recorded breeding in that year) to 67% in 2002 (Table 2.5). When the analysis was restricted to Areas G and B, the proportion breeding figures ranged from 37% in 1994 to 71% in 2002. The number of birds recorded breeding peaked in 1996.

Nonbreeders

Thirty-nine percent of the adult *Apollo Sea* survivors that were re-sighted at Dassen Island were never recorded breeding, neither at Dassen Island nor any other colony, in

the period from release in 1994 until March 2005 (Table 2.3). When considering only the birds observed in Area G and B, this proportion dropped to 30% and 26%, respectively (Table 2.3). Thirty one percent of the nonbreeders were observed on only one occasion at Dassen Island (Figure 2.8), compared with 7% of the adult *Apollo Sea* breeders. The maximum number of times a nonbreeder was observed during the study period was 33 times; this penguin, S22892, was observed in every year from 1995 to 2001, and on 15 separate occasions in 1996 (Table 2.6). Nonbreeders were observed in each year, from 1994 to 2005. The number of nonbreeders re-sighted was at a maximum in 1995 and 1996, declining to two birds in 2005. Nine percent of the *Apollo Sea* nonbreeders were also observed at other colonies, mostly (84%) at Robben Island.

Seventy-seven percent of all observations relating to nonbreeders were of birds on landing beaches, as opposed to in breeding colonies. For 2 246 de-oiled penguins for which observations of the number of times a penguin had been re-sighted on a beach (B) and the number of times it had been re-sighted in a breeding colony (C) were available (birds also observed at other colonies were excluded) a generalised linear model (logistic regression) for the probability (p) of being a nonbreeder was

$$\text{logit}(p) = 1.765 + 0.0421B - 1.5404C$$

The standard errors of the three coefficients were 0.011 (z=16.0, P<0.001), 0.0178 (z=2.37, P=0.018) and 0.0793 (z=–19.4, P<0.001). The positive coefficient of B indicated that the more frequently the penguin was seen on the beach the more likely it was to be a nonbreeder, and the negative coefficient of C indicated that the more frequently the penguin was seen in the colony, the less likely it was to be a nonbreeder. This model accounted for 49% of the deviance.

Of the nonbreeders that were observed in a breeding colony, 268 (29% of the total number of nonbreeders re-sighted during the study) were recorded on a nest site (Table 2.7). This percentage increased to 35% and 41% when the analysis was restricted to Area G and B, respectively Table 2.7).Of the activities recorded for each re-sighting, the "Pair" activity is the closest to a breeding activity. This activity describes a pair of birds actively defending a nest site (Table 2.1), and normally forms part of the pair formation phase preceding egg-laying (Randall & Randall 1981). Forty-two percent of the

nonbreeders observed on a nest were re-sighted as a pair, the remaining birds being recorded either loafing and/or moulting on the nest (Table 2.7). The percentages for Area G and B were 46% and 37% respectively. The sum of the birds recorded in each of these categories exceeds the total number of birds observed on nests because some of the birds were recorded more than once on a nest and in more than one of the categories during the study.

Birds recovered dead

Of the 2 375 adult *Apollo Sea* birds re-sighted at Dassen Island, 43 (1.8%) had been found dead and reported to SAFRING by the end of March 2005. Twenty-six of these were birds which had been recorded breeding after being de-oiled, and 17 were nonbreeders, 1.9% of both the total number of breeders (1459) and nonbreeders (916) that were observed at Dassen Island. Seventeen of the 26 recoveries of breeders (62%) were found at Dassen Island, with 53% of the nonbreeders being found there (Table 2.8). The remainder of the recoveries of breeders were reported from other penguin colonies in the Western Cape (two from Dyer Island, 34°41'S, 19°25'E, and one from Bird Island, Lamberts Bay, (32°05'S, 18°17'E), one from the penguin colony at Seal Island, Algoa Bay (33°51'S, 26°16'E) in the Eastern Cape, and six from non-colony locations in the Western Cape. Nine (53%) of the *Apollo Sea* nonbreeder recoveries were reported from Dassen Island, one from the penguin colony at Marcus Island (33°02'S, 17°58'E), the remainder being reported from non-colony locations in the Western Cape (Table 2.8). All of these non-colony sites were in close proximity to Dassen Island, the farthest being at Grotto Beach, Hermanus (34°25'S, 19°17'E), about 160km from Dassen Island (Figure 2.1).

Two de-oiled juvenile penguins, observed at Dassen Island after release, were recovered dead. S22481, released on 21 August 1994, was re-sighted defending a nest with one downy chick on 8 May 1995 (about nine months after having been released as a juvenile). It was observed on five subsequent occasions (never breeding), before being found dead at Dassen Island on 20 March 1997. S22821 was re-sighted on three occasions as a juvenile in 1995, on four occasions as an adult at Dassen Island in 1996 and 1997, four as an adult on Robben Island in 1997, 1998, and 2001 before being found dead at Melkbosstrand (33°43'S, 18°26'E), a mainland beach between Robben

and Dassen Islands, on 10 December 2001. It had not been recorded breeding on either island before its recovery.

Capture-Mark-Recapture Models

Model selection showed that survival in all states, and transition between states, varied over time (Model 2, Table 2.2, and Figures 2.9a, b). The best model kept survival for nonbreeders and breeders equal, but gave lower survival estimates for secondary nonbreeders. The survival difference was constant over time. Transition rates varied over time independently of one another. The probability for nonbreeders to start breeding was highest during the early years of the study and then declined (Figure 2.9b). On average, 31.5% (SE = 2.3) of the breeders became secondary nonbreeders each year, and a similar proportion (mean=29.1%, SE = 3.3) of secondary non-breeders resumed breeding (Figure 2.9b), implying a constant proportion of secondary nonbreeders in the population. Towards the end of the study, however, the proportion of penguins that stopped breeding increased and the proportion of secondary nonbreeders resuming breeding decreased, albeit marginally, implying an increasing proportion of secondary nonbreeders towards the end of the study.

Breeding birds were virtually always detected. Their re-sighting probabilities were 1 and constant over time. On the other hand, the re-sighting probabilities of nonbreeders and secondary nonbreeders varied through time; secondary nonbreeders consistently had a higher re-sighting probability (Figure 2.9c). This result suggests that similar factors affected movement and behaviour of these two groups. When banding at SANCCOB was included as the first sighting, 11% of the surviving penguins (those penguins re-sighted at Dassen Island at some point during the study period) were shown to have resumed breeding in 1994, the same year as they had been oiled (Figure 2.9b).

To obtain an independent indication of the restoration success of de-oiling penguins following the *Apollo Sea* oil spill, the results obtained from the CMR analysis were used. Excluding estimates from the end of the study period, when confidence intervals were large due to a substantially reduced sample sizes, the average annual survival rate for breeders and nonbreeders was 0.84, similar to the figure of 0.80 reported for African Penguins at Dassen Island by Whittington (2002). Together with the estimates for the probability of transition from nonbreeder to breeder each year, these estimates indicate

that 73% of the de-oiled bird observed back at Dassen Island attempted to breed, which is within the range found in the different study areas on the island by re-sighting methods.

DISCUSSION

Restoration success

Previous studies have shown that de-oiled African Penguins have as good a chance of survival in the wild as birds that have never been oiled (Underhill *et al.* 1999, Whittington 1999b, 2002). My results show that a substantial proportion of the birds that survived and were re-sighted back at Dassen Island after the *Apollo Sea* oil spill (i.e. rehabilitated) were successfully restored into the breeding population. The proportion of the rehabilitated birds that were recorded breeding was higher for the two study areas (G and B) than for the whole island. This is almost certainly due to the difficulty of capturing every breeding attempt on the island, where most of the penguins nest in burrows or under boulders, and the more intensive and systematic monitoring of nests in the two study areas. The difference in the proportion breeding between Area G and B is only marginal and is likely related to the layout of the coast relative to the colony in these two areas. Most penguins that come ashore in Area B breed in the monitored study area, whereas many of the penguins coming ashore along the coast of Area G, breed in Areas F and H (pers. obs.; Figure 2.2), which was not as intensively monitored as Areas G and B, potentially underestimating the proportion of birds observed in Area G that bred. Given that every nest site in the breeding colonies of Area G and B was checked monthly from November 1994 until the end of 1995 and twice a month from 1996 until March 2005, it is likely that almost all of the birds that did breed in these areas would have been detected.

The proportion of de-oiled penguins recorded breeding in this study, whether using the 61% for the whole island or 74% for study Area B, were significantly higher than results previously reported for African Penguins. Morant *et al.* (1981) found between zero and 29% (mean = 20%) of the rehabilitated penguins (those seen alive back at their breeding colonies) breeding after seven oiling incidents in the 1970s. The higher proportion recorded breeding in this study is likely to be due to the higher intensity and longer

period of monitoring after the *Apollo Sea* spill. It may also be in part due to improved treatment methods at SANCCOB, as reflected by the greatly improved release rates (proportion of oiled birds admitted to SANCCOB that were released in a healthy state) between 1970 and 1994. In the 1970s the annual average release rate was 52%, increasing to 78% in the 1990s (Nel *et al.* 2003). As far as I am aware, this is the first study to assess the restoration success of de-oiled seabirds that spans more than a decade. I am also unaware of any other study of oiled birds that reports such high survival of de-oiled birds to reproduction.

This study focused on the proportion of birds re-sighted at Dassen Island (successfully rehabilitated) that were recorded breeding, rather than the proportion of birds that were released from SANCCOB. The proportion of de-oiled penguins released after the *Apollo Sea* oil spill which "belonged" to Dassen Island is unknown. The majority (80%) of the oiled birds were removed from Dassen Island, the remainder coming from Robben Island (15%) and other island colonies and mainland beaches (5%) (Dehrmann 1994a, b). However, an unknown proportion of the oiled birds that were removed from Dassen Island may have been birds from other colonies that merely hauled out at the nearest colony (Dassen Island) once they became oiled (Underhill *et al.* 1999), making extrapolations difficult.

Although over 10% of the de-oiled penguins resumed breeding within a year of release, the pattern of cumulative restoration suggests that the rate of restoration was both slower and more sporadic than the rate at which birds were observed for the first time (Figures 2.4, 2.5 and 2.6). It also shows that although the proportion breeding estimates are probably minima, the cumulative totals approached an asymptote two and a half years after the de-oiled birds were released and further monitoring is unlikely to change the proportion breeding results even marginally. Indeed, 76% of the adults from Area G and B that were successfully restored had been recorded breeding by the end of 1996. The slower pattern of restoration relative to the pattern of first re-sightings suggests a slight delay (median interval = 11 months) between the first sighting of the bird back at the colony and its first recorded breeding attempt. This delay may be due to the loss of their mate and the time required to establish a new pair-bond (Fry *et al.* 1986, Kerley & Erasmus 1987, Giese *et al.* 2000, Chapter Five) and a disruption of the breeding and moult phenology and synchrony of affected birds (Underhill & Crawford 1999, Hemming

2001, Chapter Three). It is also possible that sub-lethal impacts of ingested oil may have contributed towards physiological impacts which suppressed breeding activities of some individuals temporarily (Butler *et al.* 1988, Walton *et al.* 1997). The step-wise pattern in the rate of cumulative restoration reflected peaks in breeding activity and the time of the annual penguin census, when every active penguin nest was checked for banded birds. The number of "new" *Apollo Sea* breeders and the gradient of the cumulative restoration graph increased during these periods. Although there appeared to be a slight delay in breeding activities for many of the birds, some individuals were recorded breeding within a month of their release. One bird (T0764) was observed back at its nest site on Robben Island with two downy chicks a day after it had been released at Silwerstroomstrand (Underhill *et al.* 1999). Its mate (S1309) was not oiled in the spill and continued rearing the two chicks while T0764 was being cleaned and treated.

It is not known what proportion of the adult-plumaged penguins released after the *Apollo Sea* spill was of breeding age. Juvenile African Penguins moult into adult plumage from 12 to 23 months after hatching (Randall 1989, Kemper & Roux 2005), but generally only start breeding when they are three years or older, with a mean age of first breeding at Dassen Island of 4.6 years (Whittington *et al.* 2005c). This means that some of the birds classified as adults may not have been breeding birds at the time of the spill. However, given the length of the study, and the similar survival rates for birds in their second and subsequent years (Randall 1983, Whittington 2002), the overall results are unlikely to be affected. Further, the oil spill occurred at the peak of the breeding season for African Penguins in the Western Cape (Marine and Coastal Management and unpubl. data, Chapter Three), so it is likely that the majority of the birds affected would have been breeding adults or birds about to recruit into the breeding population.

It is also possible that a small number of the birds re-sighted at Dassen Island were resident breeders at other colonies. A small percentage (1.9%) of the birds re-sighted at Dassen Island was recorded breeding at other colonies. The majority of these bred at Robben Island, and two at Jutten Island. These are likely to have been transient birds visiting Dassen Island in between breeding activities (Whittington *et al.* 2005b). Eight individual African Penguins have been recorded breeding at more than one locality, all of them *Apollo Sea* survivors, and all of them having bred at least once at Dassen Island (Whittington *et al.* 2005a). However, these records are considered to be exceptional, and

breeding at more than one colony is an extremely rare event (Randall *et al.* 1987, Whittington *et al.* 2005a). The re-sighting of transient birds at Dassen Island may have introduced some bias to the proportion breeding results. If these birds were resident breeders at colonies that received a relatively low level of monitoring, it is possible that breeding attempts by these birds were not detected, thereby underestimating the restoration success. However, given the relatively low incidence of birds moving to colonies other than Robben Island, where observer effort was relatively high, this bias is likely to be minimal.

A minimum of 45% of the birds recorded breeding were still alive and being observed at Dassen Island after five years of release, and 4% were known to have survived into their ninth year. This confirms that the restoration success was not of a short-term nature. Not only were these birds observed alive, but more than half (between 59% and 71%) of the de-oiled *Apollo Sea* adults that were observed each year from 1998 to 2005 were recorded breeding.

The proportion of juvenile birds observed back at Dassen Island and recorded breeding was lower than that of birds in adult plumage. This is not surprising given that the annual survival rate of African Penguins in their first year of life is lower than that of adults (Randall 1983, La Cock *et al.* 1987, Randall 1989, Whittington 2002, but see La Cock & Hänel 1987). Most African Penguins start breeding from the age of four or five (Crawford *et al.* 1999, Whittington *et al.* 2005c), reducing further the number of birds that survived until breeding age, and the amount of time available in the study to capture breeding attempts by these birds. The mean estimate for first year survival of penguins at Dassen Island for the period 1987–1999 was 0.38; survival in subsequent years was 0.80 (Whittington 2002). Using these estimates, 132 of the 348 (348 × 0.38) de-oiled banded juveniles would be expected to survive the first year. For the second year after release the number of birds expected to be alive would be 132 × 0.8 and so on for subsequent years. It would therefore be expected that 84 of the de-oiled birds released in juvenile plumage to have survived into their fourth year, and 68 birds to have survived into their fifth year, thus reaching breeding age. The 22 birds in this group that were recorded breeding represent 26% of the birds expected to survive to their fourth year and 32% of the birds expected to survive to their fifth year. Juvenile African Penguins disperse from natal colonies after fledging (Randall *et al.* 1987, Hockey *et al.* 2005), and so many of

the juvenile penguins oiled in the vicinity of Dassen Island during the *Apollo Sea* spill are likely to have been far away from their natal colony at the time. Of the 10 000 penguins oiled in the *Apollo Sea* incident, 215 had been flipper-banded prior to the spill. For those birds whose natal or breeding colony was known, the majority (84%) were from Dassen and Robben Islands; for the remainder, the natal or breeding colonies spanned almost the entire range for the species, from Bird Island, Algoa Bay (33°50'S, 26°17'E), 730km to the east, to Ichaboe Island, Namibia (26°17'S, 14°56'E), 900km to the north (Underhill *et al.* 1999, Whittington 2002). In addition, although juvenile African Penguins usually recruit to their natal colonies, first-time breeders appear to be able to recruit to non-natal colonies if food is more plentiful there (Crawford *et al.* 1995, 1999, Crawford 1998, 1999, Whittington *et al.* 2005a). It is likely the proportion of de-oiled juvenile penguins that returned to breeding colonies that were not as intensively monitored was larger than for adult-plumaged penguins, increasing the likelihood that breeding attempts by these birds were not detected.

Nonbreeding

A substantial proportion of the de-oiled adult penguins released after the *Apollo Sea* spill resumed breeding, and bred for many years after the spill. However, between 26% and 39% of the de-oiled birds which were successfully rehabilitated (i.e. re-sighted at Dassen Island) never bred again. The case for nonbreeding is further supported by multiple observations of many of these birds in the intensively monitored study colonies over long periods of time, some having been re-sighted in 10 of the 12 available years (1994–2005).

It is possible that some of these birds did breed, and their breeding attempts were not detected. Thirty-one percent of the nonbreeders were observed only once at Dassen Island. Some (9%) of the nonbreeders that were observed on only one occasion were also observed at other breeding colonies (mostly Robben Island), and may have been transient visitors to Dassen Island when re-sighted there. However, a similar percentage (10%) of the *Apollo Sea* breeders was observed "visiting" other colonies. In both groups, the colony "visited" on most (>80%) of the occasions was Robben Island, where observer effort was relatively high during the study period, and where most breeding attempts should have been detected (P.A. Whittington pers. comm.).

Some of the nonbreeders attempted to breed, but were never successful. One third of the nonbreeders were re-sighted at least once on a nest site, although it is likely that at least some of these birds fled into empty nest sites (in burrows or amongst boulders) as I approached the colony, and were erroneously identified as occupying the nest site when I arrived at the nest in question. African Penguins are vulnerable to disturbance at their breeding colonies (Frost *et al.* 1976, Hockey & Hallinan 1981, van Heezik & Seddon 1990), and penguins loafing at the outskirts of a colony or within it were often observed fleeing away from the observer into nests. Those birds (16% of nonbreeders in Area G) re-sighted defending a nest with another penguin (its mate), are unlikely to have been intruders and represent a more accurate reflection of the number of nonbreeders attempting to breed. Most of the nonbreeders spent little time within the breeding colonies, and were seen much more often along the shore, in contrast to breeders that were much more likely to be re-sighted within a breeding colony. Similarly, Adélie Penguin nonbreeders spend fewer days at the rookery than breeders (Ainley *et al.* 1983). African Penguins nest in colonies of varying density, with high rates of aggression between adults (Eggleton & Siegfried 1979). For birds that are unable to breed, spending time in a breeding colony may not only be unproductive, but also risky.

It was not possible in this study to compare the de-oiled *Apollo Sea* birds to an un-oiled control group. Large scale oil spills generate abnormal samples of birds, and it is not possible to establish a proper control group because no group of penguins at colonies is equivalent in terms of age structure and other demographic parameters. Long term studies of penguins have shown that the proportion of birds breeding varies with age, differs between species, and is dependant on age at first breeding and other life history parameters (Williams 1995b, Hamer *et al.* 2002, Weimerskirch 2002). The majority of Adélie Penguins only start breeding from four to six years of age, the proportion increasing to 94% of 12 year old birds (Ainley 1978). The proportion of adult Yellow-eyed Penguins *Megadyptes antipodes* breeding reaches its peak at the age of four (Richdale 1957). A long-term study of African Penguins at Robben Island found that the most commonly recorded age at first breeding was four, with 80% of known aged birds breeding by age six (Crawford *et al.* 1999). In the latter study, it was thought that birds recorded breeding for the first time at ages older than six, had bred earlier without being observed, and so it was assumed that 100% of birds older than four were breeders. It is possible that some of the de-oiled *Apollo Sea* nonbreeders bred unnoticed, but given the

length and intensity of the study, the evidence provided indicates that oiling has inhibited breeding for a proportion (maximum 39%) of the rehabilitated birds.

Sub-lethal impacts of oil contamination

Although I am confident that oiling inhibited breeding for some birds, the mechanisms involved are less certain. Oil contamination has been shown to impact the breeding biology of penguins and other seabirds in a variety of ways. The effects appear to be highly species-and dose-specific. Low levels of oiling of Magellanic Penguins *Spheniscus magellanicus* interfered with the circulation of reproductive hormones, which led to lower rates of nest establishment and suppression of egg laying (Fowler *et al.* 1995). Ainley *et al.* (1981) orally dosed Cassin's Auklets *Ptychoramphus aleuticus* with bunker fuel oil and found that this led to a reduction in the proportion of birds laying eggs, and reduced hatchability in a dose-dependent manner. Similarly, Wedge-tailed Shearwaters *Puffinus pacificus* exposed both internally and externally to weathered crude oil exhibited progressively reduced breeding with increases in the dosage of oil applied (Fry *et al.* 1986). Other studies indicate that there is often long-term damage to key organs, especially the liver and kidneys, as a result of the ingestion of even minute quantities of oil (Fry & Lowenstine 1985, Nisbet 1994). It is also thought that oiling (and handling of birds at rehabilitation centres) may induce immunosuppressive mechanisms that increase the bird's risk to parasite-mediated infections, as well as reproductive problems (Briggs *et al.* 1996, 1997). Most of the studies reporting sub-lethal effects of oil exposure have focussed on the short-term effects of oiling on breeding biology, seldom tracking birds over more than one season. A few studies have followed seabirds over two seasons, with contrasting results. Small doses of oil fed to breeding Leach's Storm-Petrels *Oceanodroma leucorhoa* resulted in significantly reduced breeding productivity in the season that the birds were oiled, but no effect was detected the following season (Butler *et al.* 1988). On the other hand, Fry *et al.* (1986) reported greatly reduced reproduction in Wedge-tailed Shearwaters following dosing in the season of treatment, as well as residual effects in the second season that were attributed to the disruption of pair-bonds. Giese *et al.* (2000) found measurable differences in reproductive success in two breeding seasons following the release of de-oiled Little Penguins after the *Iron Baron* oil spill.

Stress related suppression of breeding may in part explain the short-term delay in breeding shown by some of the de-oiled *Apollo Sea* birds, but it is unlikely to be the cause of permanent nonbreeding. Penguins would likely show lower survival rates if they were exposed to continued stress. Whittington (1999a, 2002) showed that survival rates for de-oiled African Penguins are similar to un-oiled birds, and this study reported similar survival rates for *Apollo Sea* breeders and nonbreeders, in terms of both the CMR analysis and flipper-band recoveries. It is much more likely, then, that nonbreeding in de-oiled African Penguins is related to toxic effects on the reproductive organs, effectively sterilizing these birds. The nonbreeders may have been the birds that suffered the worst degree of oiling; above a threshold value of oiling (and oil ingestion), the negative impacts of the oil on the reproductive organs may not be possible to reverse through cleaning and treatment. Goldsworthy *et al.* (2000) found that degree of oiling (and its influence on capture mass and body condition) was the most important variable contributing towards the significantly lower survival of de-oiled Little Penguins, when compared with un-oiled birds, after the *Iron Baron* oil spill. Although the birds were cleaned, treated and released in seemingly healthy condition, birds that experienced lower levels of oiling had the greatest probability of survival, indicating that not all of the deleterious effects of oil contamination were overcome by treatment. Birds in poor condition are known to be more susceptible to the toxic effects of oil than birds in good condition (Fry & Lowenstine 1985). It is likely that the impacts are more complicated than this because the toxic effects of oil may interact synergistically with other stressors (Leighton 1991), such as the capture, handling and treatment of the birds as well as other environmental stressors.

Intermittent breeding and possible costs of reproduction

The relatively high rate at which breeders became secondary nonbreeders each year and the lower survival rate of these secondary nonbreeders, indicated that oiling may have also affected the *Apollo Sea* breeders. In this study secondary nonbreeding refers to nonbreeding in birds that had previously bred, which is better termed intermittent breeding to distinguish these birds from the *Apollo Sea* nonbreeders. Life-history theory predicts trade-offs between reproduction and survival and between present and future reproduction in a resource-limited environment (Stearns 1976, McNamara & Houston 1996). Several studies of seabirds have found high levels of intermittent breeding (Furness & Monaghan 1987, Chastel *et al.* 1995, Weimerskirch 2002). Some studies

have interpreted intermittent breeding as an adaptive strategy to preserve future reproductive value and lifetime reproductive output (Wooller *et al.* 1989, Aebischer & Wanless 1992), while others have suggested that intermittent breeding relates to differences in individual quality (Harris & Wanless 1995, Cam *et al.* 1998). The incidence of intermittent breeding at population level is often correlated with environmental conditions, such as weather and food availability (Hays 1986, Crawford & Dyer 1995, Crawford *et al.* 1999, Simeone *et al.* 2002, Crawford 2003). Food availability, and particularly the abundance and distribution of shoaling epipelagic fish (principally Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax*), has been shown to determine the proportion of African Penguins breeding each year (Crawford & Dyer 1995, Crawford *et al.* 1999, 2001). At Robben Island, the estimated proportion of experienced adults that did not breed ranged from 30% in 1988 to 0% in 1991 (Crawford *et al.* 1999). At Stony Point (34°22'S, 18°54'E) 20% of the total number of breeding attempts possible were missed in the periods 1982–1986 and 1989–1996, 70% of these skipped attempts occurring in years when the colony size was decreasing or when breeding success was low (Whittington *et al.* 1996). The incidence and degree of intermittent breeding of *Apollo Sea* breeders were higher throughout this study compared with the figures reported above for African Penguins. Moreover, this study took place during a period of significantly increased availability of Anchovy and Sardine, when rapid increases in the sizes of African Penguin breeding colonies in the Western Cape, including Dassen Island, were reported (Wolfaardt *et al.* 2001, Barange *et al.* 2004, du Toit *et al.* 2004, Chapter Four). Increases in the number of African Penguins breeding during this period are thought to result from an increased proportion of experienced birds breeding and higher reproductive success (Crawford *et al.* 2006). The relatively high incidence of intermittent breeding for *Apollo Sea* birds during this period is therefore more likely explained by the impacts of oiling on the condition and overall fitness of these birds than by the environmental conditions (food availability) alone.

A further line of evidence for sub-lethal effects of oiling on the *Apollo Sea* birds is the lower estimated survival rate of secondary nonbreeders when compared with both *Apollo Sea* breeders and nonbreeders. The negative relationship between breeding and subsequent survival appears to indicate the existence of a cost of reproduction for these birds. This is supported by the finding that the proportion of de-oiled *Apollo Sea* birds that stopped breeding increased, and the proportion of the secondary nonbreeders

resuming breeding decreased, towards the end of the study, suggesting senescence both in survival and reproduction. Due to the moratorium on flipper-banding African Penguins, the de-oiled *Apollo Sea* birds could not be compared to an un-oiled control group. Additional support for a cost of reproduction amongst de-oiled birds comes from the survivors of the *Treasure* oil spill of 2000. De-oiled birds from the *Treasure* spill had similar survival rates to the un-oiled birds that were evacuated during this spill, until they started breed, from which point on the survival of de-oiled birds was significantly lower than evacuated (un-oiled) birds (Chapter Six). Dann *et al.* (1995) found no reproductive cost to Little Penguins in terms of survival or residual reproductive value. In contrast, in a two year study after the *Iron Baron* oil spill, oiled-rehabilitated Little Penguins were found to weigh less than non-oiled birds after breeding in both seasons, suggesting that breeding may have exerted a higher energetic cost to oiled-rehabilitated individuals (Giese *et al.* 2000, Goldsworthy *et al.* 2000). Taken together, these results suggest that, despite high post-release survival and restoration success of de-oiled birds, reproduction exacts a higher energetic cost to de-oiled penguins than to un-oiled individuals.

Sex differences

African Penguins are difficult to sex visually in the field. In this study only birds that were monitored as part of the breeding success study were sexed (Chapter Five), and so for the majority of birds, it is not known whether the effects of oiling were different for males and females. Other studies on penguins have shown that the impacts of oil contamination are greater for females than males. In Magellanic Penguins, reduction in body mass and levels of sex hormones, as well as higher levels of corticosterone in oiled females relative to oiled males and un-oiled birds, suggests a higher energetic cost of oiling for females (Fowler *et al.* 1995). Post-release survival of oiled-rehabilitated Little Penguins is lower in females than males (Goldsworthy *et al.* 2000), and breeding success was found to be lowest in those nests that contained a de-oiled female (Giese *et al.* 2000). It is possible that female African Penguins are more susceptible to oil impacts, but I failed to detect a difference in breeding success between *Apollo Sea* males and females (Chapter Five).

CONCLUSION

These findings indicate substantially higher restoration rates than previously reported for the species (Randall *et al.* 1980, Morant *et al.* 1981), and represent, as far as I am aware, the most successful restoration results for oiled seabirds anywhere. Several factors contribute towards this success, including the robust nature of the African Penguin (facilitating their ability to withstand capture and repeated handling), the proximity of the colonies of penguins that were oiled in the *Apollo Sea* spill to the rehabilitation centre, and the relative ease with which flipper-banded penguins can be monitored. While it is clear that the high level of restoration reported justifies the importance of de-oiling African Penguins as a conservation management tool, the results show that oil contamination does exert sub-lethal impacts that may reduce long-term reproductive output. Consequently, the conservation status of African Penguins would be better served by reducing the occurrence of oil spills in the first place, especially in the vicinity of seabird colonies.

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Table 2.1 Description of activities recorded for each re-sighting of banded African Penguins at Dassen Island. The activities are mutually exclusive, so for each re-sighting only one of the range of activities is included.

Activity	Description
Chick(s)-B	Bird brooding/guarding 1 or 2 blue chicks
Chick(s)-D	Bird brooding/guarding 1 or 2 downy chicks
Chick-B	Bird guarding 1 blue chick
Chick-B/Pair	a pair with guarding 1 blue chick
Chick-D	Bird brooding/guarding 1 downy chick
Chick-D/Pair	A pair brooding/guarding 1 downy chick
Chicks-B	Bird guarding 2 blue chicks
Chicks-D	Bird brooding/guarding 2 downy chicks
Chicks-D/Pair	A pair brooding/guarding 2 downy chicks
Egg	Bird incubating 1 egg
Egg&Chick	Bird incubating 1 egg and brooding 1 chick
Egg&Chicks	Bird incubating 1 egg and brooding 2 chicks
Egg(s)	Bird incubating either 1 or 2 eggs
Egg/Pair	A pair with one of the individuals incubating 1 egg
Eggs	Bird incubating 2 eggs
Eggs&Chick	Bird incubating 2 eggs and brooding 1 chick
Eggs/Pair	A pair incubating 2 eggs
Evacuated	Bird evacuated during the Treasure oil spill
Intruder	Intruder in a nest
Loafing	Bird alive and well but not engaged in any of the other activities
Loose ring	Loose ring found - either lost or from a carcass
Moulting	Bird moulting
Moulting/Pair	Bird moulting with another penguin in the burrow/nest
Not recorded	No activity recorded
Pair	Pair without eggs or chicks
Released on Dassen	Caught and released back on the island during the *Treasure* oil spill rescue operations
SANCCOB	Oiled and sent to SANCCOB during the *Treasure* oil spill rescue operation

Table 2.2 Summary of model selection of multi-state capture-mark-recapture analysis for de-oiled African Penguins at Dassen Island, 1994-2005. The models consisted of nine parts: three parts modelling survival in each breeding state (S_n, S_b, S_s for non-breeder, breeder and secondary non-breeder, respectively); three parts modelling the recapture rates in these states (P_n, P_b, P_s); and three parts modelling transitions between states (ψ_{nb}, ψ_{bs}, ψ_{sb}, see Figure 2.3). All components were modelled as variable over time (t) or constant (.). Equality of survival or recapture in different states is indicated by = between the relevant model parts, and // denotes models which enforced parallel time variation in two model components. The models were assessed by Akaike's Information Criterion (AICc), and the difference between each model and the best one is given (Delta AICc). The relative performance of each model compared to the other ones in the set is measured by the Akaike weight (*w*), and this weight is used in the model averaging process. *K* is the number of parameters.

	Model	AICc	Delta AICc	*w*	*K*	Deviance
1	$S_n(t)=S_b(t)//S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16852.363	0.000	0.454	69	4666.026
2	$S_n(t)=S_b(t)//S_s(t)P_n(t)//P_s(t)P_b(.)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16852.430	0.067	0.439	60	4684.454
3	$S_n(t)=S_b(t)S_s(t)P_n(t)//P_s(t)P_b(.)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16855.838	3.475	0.080	69	4669.501
4	$S_n(t)=S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16858.151	5.788	0.025	78	4653.402
5	$S_n(.)S_b(t)//S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16863.296	10.933	0.002	79	4656.498
6	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16868.503	16.140	0.000	86	4647.345
7	$S_n(t)=S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)//\psi_{sb}(t)$	16875.145	22.782	0.000	69	4688.809
8	$S_n(t)=S_b(t)=S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16878.365	26.002	0.000	69	4692.029
9	$S_n(t)S_b(t)S_s(.)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16881.210	28.847	0.000	79	4674.412
10	$S_n(t)S_b(t)=S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16882.619	30.256	0.000	78	4677.870
11	$S_n(t)= S_s(t)S_b(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16882.727	30.364	0.000	78	4677.978
12	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(t)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16884.953	32.590	0.000	94	4647.345
13	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(.)$	16887.157	34.794	0.000	79	4680.360
14	$S_n(t)S_b(.)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16890.449	38.086	0.000	78	4685.700
15	$S_n(t)S_b(t)S_s(t)P_n(t)P_b(.)P_s(t)\psi_{nb}(t)\ \psi_{bs}(.)\ \psi_{sb}(t)$	16892.493	40.130	0.000	78	4687.744
16	$S_n(t)S_b(t)S_s(t)P_b(.)P_n(t)=P_s(t)\psi_{nb}(t)\ \psi_{bs}(t)\ \psi_{sb}(t)$	16897.744	45.381	0.000	77	4695.043
17	As model 6, but no transients effect	16918.851	66.488	0.000	77	4716.150

Table 2.3 Numbers of rehabilitated adult *Apollo Sea* African Penguins observed and recorded breeding at Dassen Island. September 1994 until March 2005.

	Whole Island		Area G		Area B	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Number observed	2375[a]	55	975	19	699	13
Number recorded breeding at Dassen	1414	20	659	9	513	6
Number recorded breeding at other colonies	45	2	19	0	2	1
Total recorded breeding	1459	22	678	9	515	7
Number not recorded breeding	916	33	297	10	184	6
Number nonbreeders observed at other colonies, but not breeding	84	12	27	4	17	4

[a] - excludes 69 birds whose bands were removed due to damage to flippers (see text)

Table 2.4 De-oiled African Penguins from the *Apollo Sea* spill that were recorded breeding in more than eight of the twelve study years at Dassen Island. The number of times the bird was observed breeding per year is also included. Multiple breeding observations within a year do not indicate separate breeding attempts because birds were often re-sighted breeding (incubating eggs or brooding chicks) on more than one occasion during a breeding attempt.

	Number of breeding observations											
Band number	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
S20672	1	0	7	2	2	3	1	4	1	5	0	0
S20882	0	2	5	2	3	6	3	5	3	7	0	0
S20886	0	1	4	6	6	10	6	6	3	3	1	0
S20894	1	3	4	2	1	9	2	1	1	0	0	0
S21225	1	3	10	9	3	10	4	6	3	3	0	0
S21244	0	0	5	1	1	6	8	4	3	6	12	1
S21338	0	3	3	2	2	3	1	3	3	3	0	0
S21585	0	0	5	4	4	2	2	4	2	4	3	0
S21630	0	2	3	1	3	3	3	4	6	3	1	0
S21647	0	3	4	1	4	4	2	3	2	1	0	0
S21672	0	1	1	2	2	1	2	4	2	2	0	0
S21739	0	2	7	0	4	4	3	4	3	7	3	0
S21809	0	1	3	3	0	6	1	2	2	4	2	0
S21888	0	3	4	5	1	4	1	0	1	7	8	0
S21894	0	3	6	10	1	7	2	4	1	2	0	0
S22111	0	2	1	4	2	1	3	1	1	0	0	1
S22121	0	2	2	4	2	7	3	0	1	9	3	0
S22137	0	7	8	9	5	1	2	7	4	3	0	0
S22158	0	1	4	4	6	4	3	3	4	1	0	0
S22309	0	4	4	2	6	10	3	0	1	3	3	0
S22374	0	1	3	5	2	7	7	4	2	8	0	0
S22400	0	3	4	2	2	1	7	3	2	4	7	0
S22464	0	1	4	6	2	1	3	2	1	3	0	1
S22490	0	2	6	5	7	6	3	7	1	3	0	0
S22507	0	2	4	0	2	4	6	1	2	1	3	4
S22517	0	1	2	11	6	2	6	5	2	2	4	0
S22911	0	0	1	2	4	3	1	6	3	8	11	2
S22942	1	3	2	0	4	2	1	3	1	2	3	0
S22954	0	2	5	8	6	9	5	3	5	1	0	0
S23192	0	3	4	4	2	2	1	1	0	1	4	0
S24110	0	0	1	2	3	1	3	6	3	6	11	0
S24223	1	1	3	6	1	1	3	1	3	1	0	0
S24268	0	0	3	1	4	4	1	5	0	3	2	3
S24354	0	1	1	3	1	8	5	1	1	3	1	0
S24689	0	0	13	2	5	4	2	3	1	1	3	0
S24940	0	1	5	7	1	4	2	4	1	1	0	0

Table 2.5 Numbers of de-oiled adult African Penguins observed and recorded breeding at Dassen Island per year.

	Whole Island			Study Colonies Area G and Area B combined		
Year	Number observed	Number breeding	Proportion breeding (%)	Number observed	Number breeding	Proportion breeding (%)
1994	307	110	35.83	241	89	36.93
1995	1649	597	36.20	1148	506	44.08
1996	1636	774	47.31	1123	629	56.01
1997	1153	488	42.32	844	439	52.01
1998	878	442	50.34	648	390	60.19
1999	700	384	54.86	517	314	60.74
2000	575	304	52.87	451	264	58.54
2001	363	235	64.74	286	195	68.18
2002	288	194	67.36	221	157	71.04
2003	150	93	62.00	116	78	67.24
2004	81	45	55.56	57	34	59.65
2005	13	8	61.54	10	7	70.00

Table 2.6 Adult African Penguin from the *Apollo Sea* spill that were never recorded breeding (nonbreeders) and were observed on more than 13 occasions at Dassen Island

	Number of times observed											
Band number	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
S18617	0	3	11	2	0	0	0	0	0	0	0	0
S18731	0	2	4	7	0	1	0	0	0	0	0	0
S20554	0	1	6	1	3	4	3	0	0	0	0	0
S20810	0	3	1	2	4	1	2	0	1	0	0	1
S21374	0	4	17	3	5	0	0	0	0	0	0	0
S21414	0	4	11	0	1	0	0	0	0	0	0	0
S21426	0	2	7	9	0	0	0	0	0	0	0	0
S21538	0	0	1	4	4	2	2	0	0	0	1	0
S21540	0	3	7	4	0	0	0	0	0	0	0	0
S21684	0	6	1	5	1	1	0	0	0	0	0	0
S21735	0	2	6	3	4	4	1	0	0	0	0	0
S21803	0	3	6	2	0	1	2	1	0	0	0	0
S21940	0	2	7	2	1	1	1	2	0	1	0	0
S21949	0	2	2	6	2	3	0	0	0	0	0	0
S21999	0	3	12	0	0	0	0	0	0	0	0	0
S22182	0	2	6	4	1	3	2	1	0	0	0	0
S22215	0	0	6	6	3	2	2	0	0	0	0	0
S22345	1	5	3	2	2	1	0	0	0	0	0	0
S22892	0	2	15	2	5	3	3	3	0	0	0	0
S22949	0	2	3	14	0	2	0	0	0	0	0	0
S24225	0	1	1	7	5	0	0	0	0	0	0	0
S24338	0	2	3	5	5	1	2	1	0	0	0	0
S24386	0	2	3	6	0	1	2	0	1	0	0	0
S24848	0	1	4	11	3	0	0	0	0	0	0	0

Table 2.7 Number of adult African Penguins from the *Apollo Sea* spill that were never recorded breeding, but were observed on a nest at Dassen Island during the period September 1994 to March 2005.

	Whole Island		Area G		Area B	
	Number of Individuals	Number of Observations	Number of Individuals	Number of Observations	Number of Individuals	Number of Observations
Number of nonbreeders re-sighted	916	3535	297	1269	184	769
Total observed on a nest	268	368	104	151	75	101
Observed as a "Pair" on a nest	113	135	48	57	28	32
Observed "Loafing" on a nest	153	190	55	71	46	56
Observed "Moulting" on nest	38	41	18	20	12	13

Table 2.8 Recoveries of dead African Penguins involved in the *Apollo Sea* oil spill and observed at Dassen Island after release

Location of recovery	Breeders	Nonbreeders
Dassen Island	16	9
Other penguin colonies in the Western Cape	3	1
Other penguin colonies outside the Western Cape	1	0
Non-colony location in the Western Cape	6	7
TOTAL	26	17

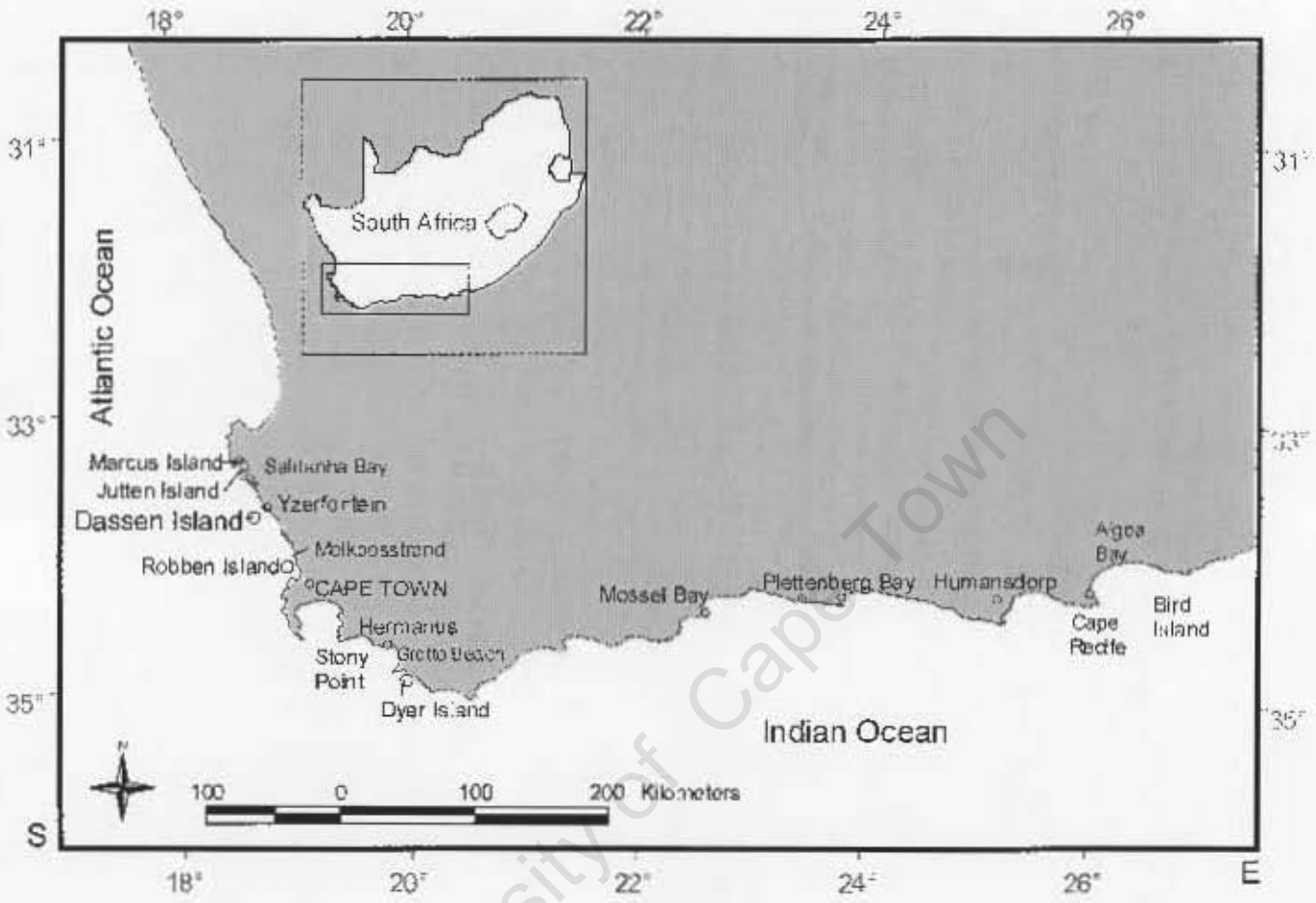

Figure 2.1 The location of Dassen Island, and other penguin colonies and localities mentioned in the text.

Figure 2.2 Locations of management and monitoring areas (Areas A–I) at Dassen Island, and the African Penguin breeding study colonies in Areas B and G.

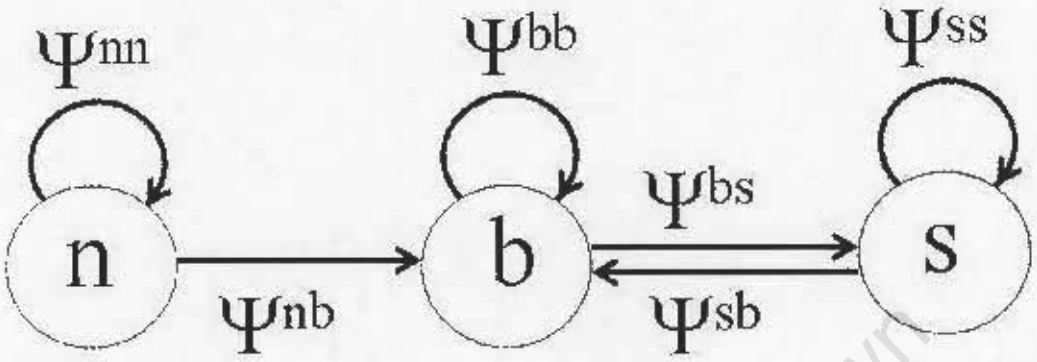

Figure 2.3 Diagram showing the states used in the multi-state capture-mark-recapture analyses for African Penguins on Dassen Island. Penguins can either be nonbreeders (n), breeders (b), or secondary nonbreeders (s). Recapture and survival rates were estimated separately for each state, and the probabilities of moving between states (ψ). The way in which the states were defined results in nonbreeders being unable to become secondary nonbreeders directly, and breeders cannot move back to the initial nonbreeder stage. These transition rates were thus fixed to zero in the analyses. See text for further details.

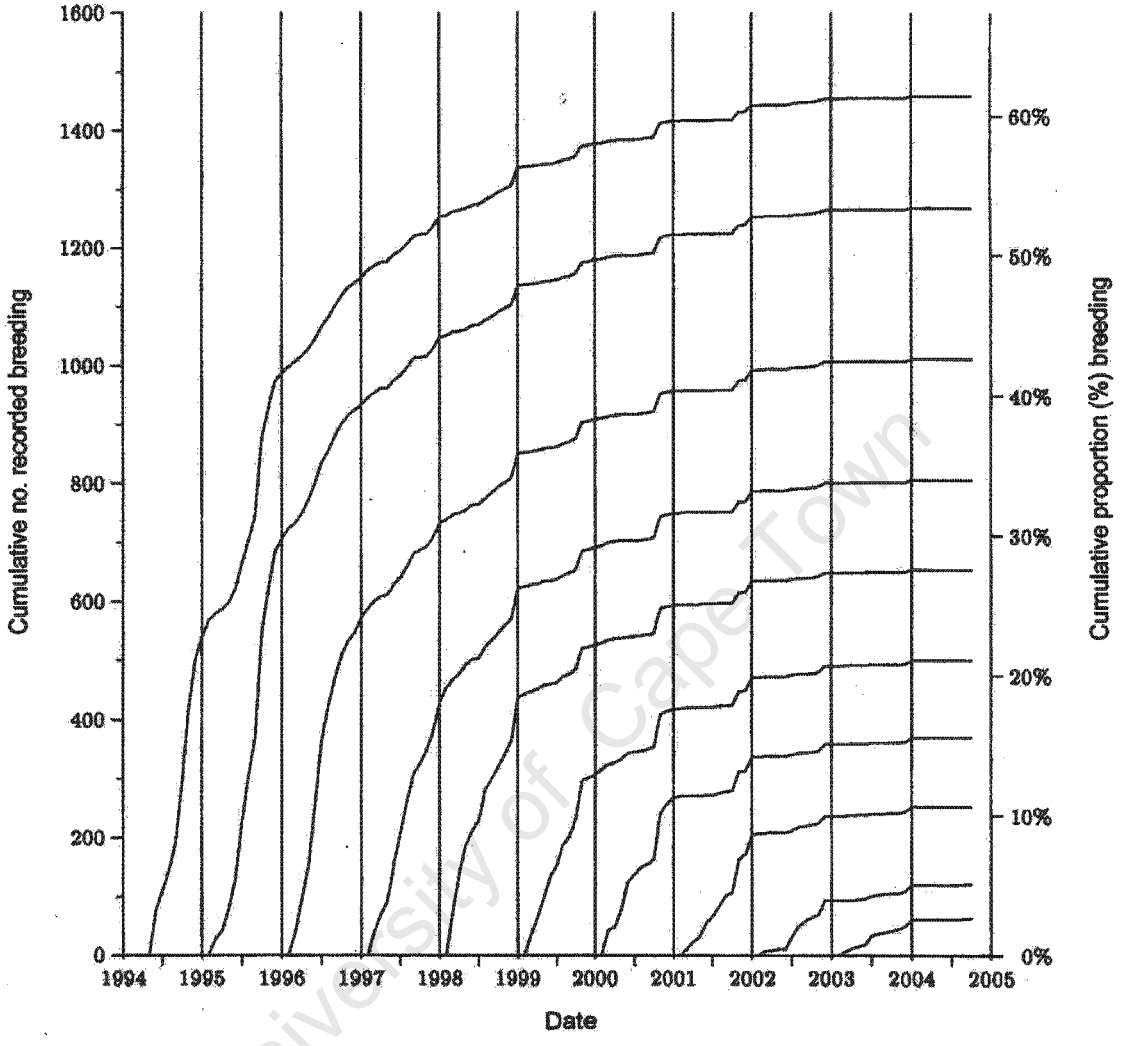

Figure 2.4 Cumulative totals of de-oiled adult African Penguins recorded breeding following the *Apollo Sea* oil spill at Dassen Island. The first line shows the overall cumulative total from the time of release (31 July 1994) until March 2005. Each line thereafter represents the number of birds recorded breeding that survived progressive periods, from at least one year after release (in the case of the line starting at 31 July 1995) up until nine years after release (for the line labelled starting at 31 July 2003). The vertical lines represent the mid-point (1 July) of each year. The proportion recorded breeding, as a percentage of the final number of adult *Apollo Sea* survivors observed at Dassen Island during the study, is shown on the right.

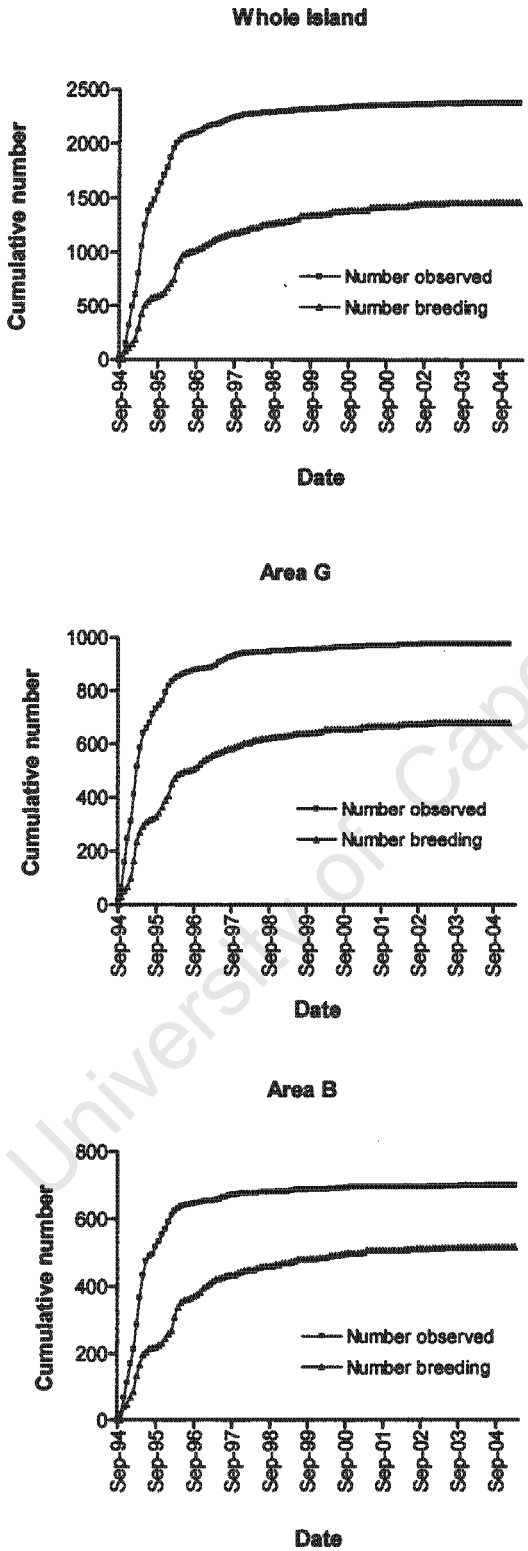

Figure 2.5 Cumulative number of de-oiled adult African Penguins from the *Apollo Sea* spill re-sighted and recorded breeding at Dassen Island after release in July 1994.

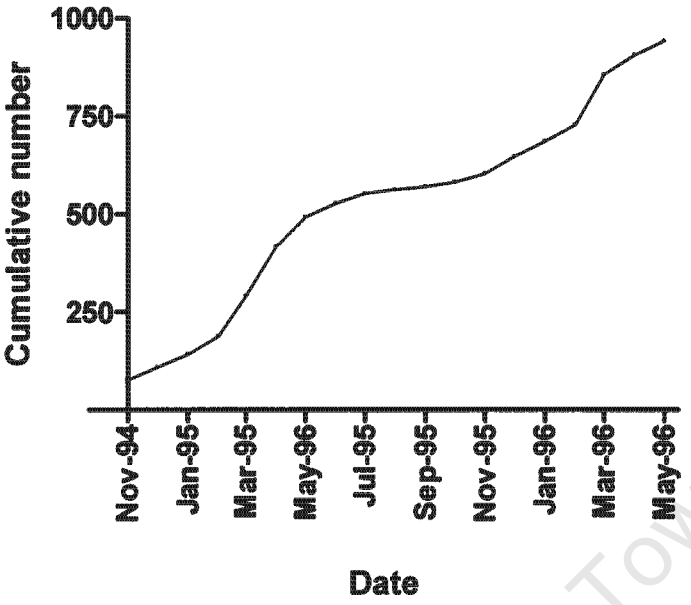

Figure 2.6 Cumulative number of de-oiled adult African Penguins from the *Apollo Sea* oil spill recorded breeding at Dassen Island. November 1994-May1996.

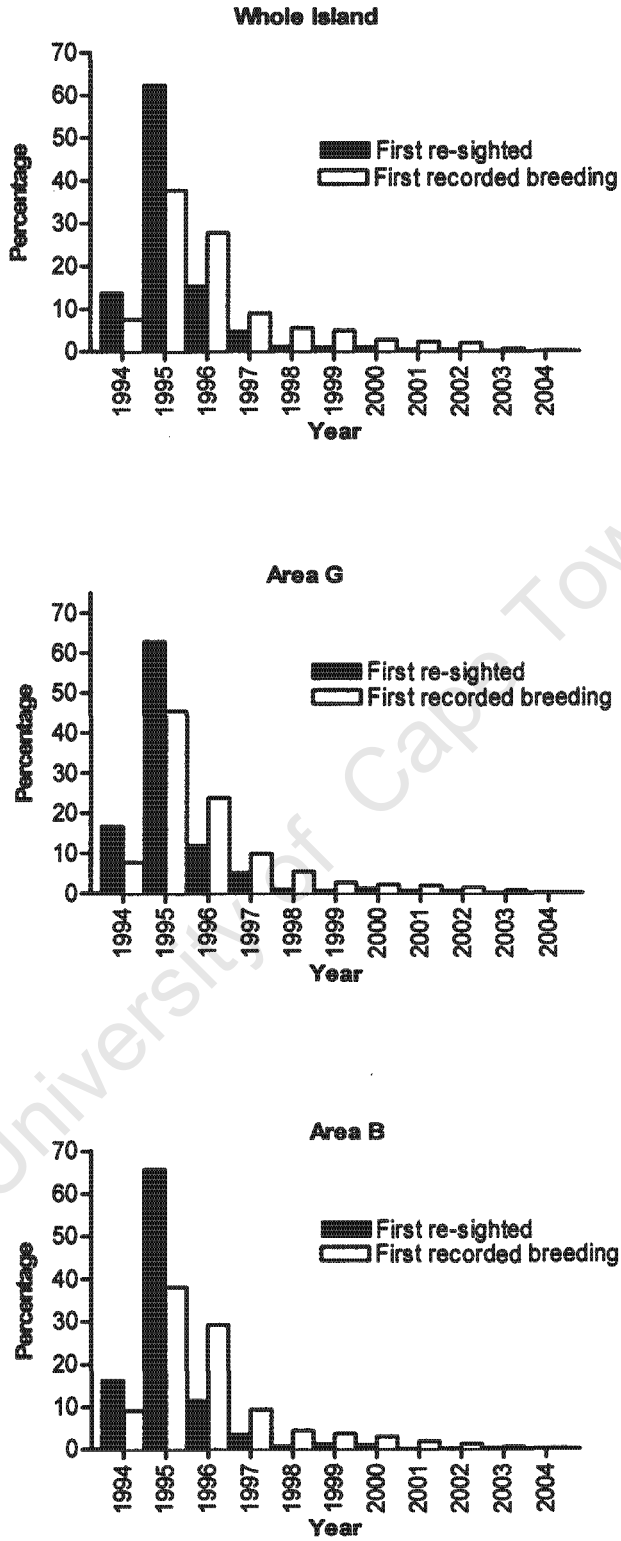

Figure 2.7 Percentage of de-oiled African Penguins from the *Apollo Sea* spill re-sighted and recorded breeding at Dassen Island for the first time after release. 1994 only includes the period September - December.

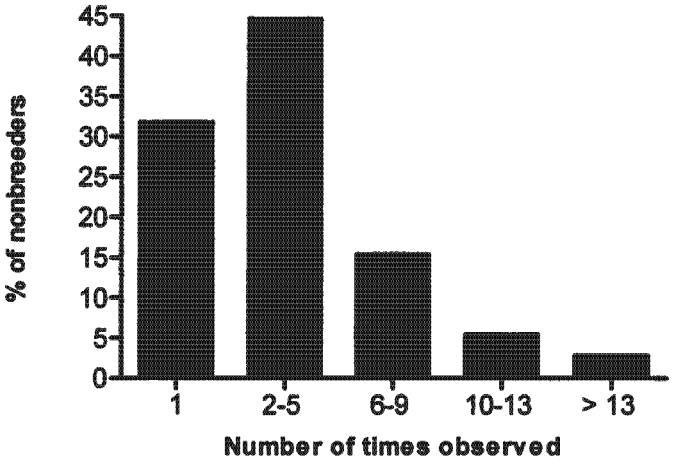

Figure 2.8 Frequency distribution of the number of times adult African Penguins that were oiled in the *Apollo Sea* spill and never recorded breeding again (nonbreeders), were observed at Dassen Island.

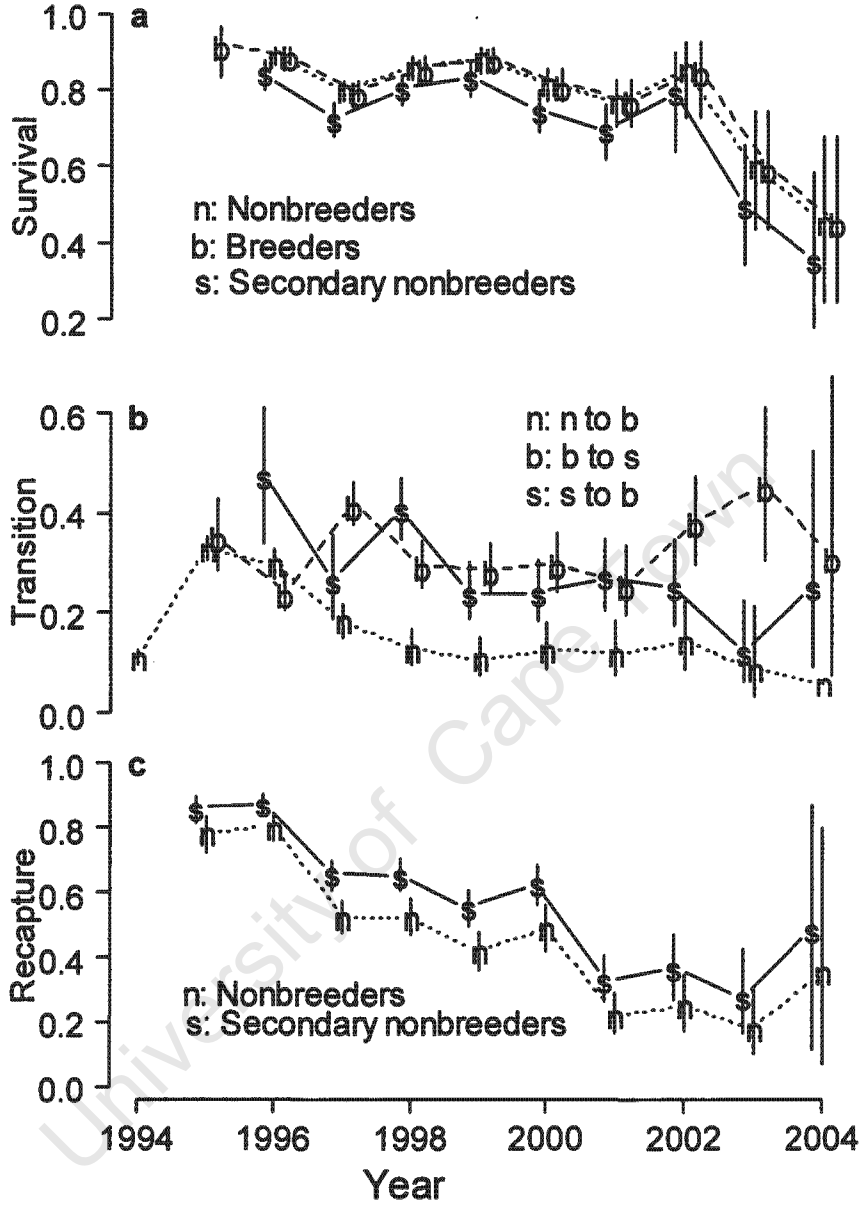

Figure 2.9 Estimates of a) survival, b) transition, and c) recapture rates of de-oiled African Penguins from the *Apollo Sea* oil spill at Dassen Island. The estimates are from Model 2 (see Table 2.2 and text for details of model selection). The vertical lines show 95% confidence intervals. Recapture rates for breeders were 1 throughout the study. Confidence intervals tend to get larger towards the end of the study because fewer individuals survived that long. The symbols are slightly offset to facilitate comparison.

Chapter Three

Breeding and moult phenology of African Penguins *Spheniscus demersus* at Dassen Island, and the impact of the *Apollo Sea* and *Treasure* oil spills

Breeding and moult phenology of African Penguins *Spheniscus demersus* at Dassen Island, and the impact of the *Apollo Sea* and *Treasure* oil spills

ABSTRACT

The breeding and moult phenology of African Penguins *Spheniscus demersus* at Dassen Island form part of a variable annual cycle. Between 1994 and 2006, African Penguins bred throughout the year. Most of this period was characterised by favourable feeding conditions. There were definite peaks in breeding activity, but these varied between years and between sub-colonies on the island, with no obvious seasonal pattern. Synchronisation of breeding activities was greater in sub-colonies with higher nest densities, suggesting that breeding phenology was influenced more by social interaction between individuals than by a wider-scale seasonal effect. Moult phenology of African Penguins at Dassen Island was highly synchronous and seasonal. Most penguins moulted between September and January. A large proportion (30%) of moult records was of birds moulting in nest sites rather than at landing beaches along the shore. The incidence of nest moulting was greatest from June to October, when sea conditions were generally rougher. The interval between successive moults ranged from 221 days to 546 days, with a mean of 349 days. Individuals moulted in the same area of the island, close to or within their breeding colony, year after year. The much greater degree of synchronisation in moult compared with breeding patterns, and the timing of moult to coincide with a relatively predictable source of food, suggest that moult, and not breeding, may represent the key driver of the annual cycle. In spite of short-term disruptions to the breeding activities of de-oiled birds, all groups of birds affected by the *Apollo Sea* (June 1994) and *Treasure* (June 2000) oil spills conformed to the pattern of breeding of the colony in which they bred. De-oiled penguins from the *Apollo Sea* spill moulted earlier and less synchronously than unaffected birds and the seasonal average for the island in 1995/96 and to a lesser extent in 1996/97, becoming more synchronous thereafter. The moult phenology of de-oiled birds from the *Treasure* spill conformed to the overall island pattern. However, penguins that were evacuated during the *Treasure* spill moulted later and less synchronously than all other penguins in the year following the spill, probably as a result of their rapid resumption of breeding activities upon their return to Dassen Island.

INTRODUCTION

Breeding and moult are critical and energetically demanding activities in the annual cycle of adult African Penguins *Spheniscus demersus*. The timing of these events should therefore coincide with periods of favourable environmental conditions, principally the availability of food (Lack 1968, Perrins 1970). For individual birds, the pattern and timing of breeding and moult are interconnected. Most penguin species moult postnuptially (Adams & Brown 1990). However, Galápagos Penguins *Spheniscus mendiculus* moult prenuptially (Boersma 1976). King Penguins *Aptenodytes patagonicus*, Humboldt Penguins *Spheniscus humboldti* and African Penguins *Spheniscus demersus* moult either before or after they breed (Cooper 1978, Adams & Brown 1990, Paredes *et al.* 2002, Simeone *et al.* 2002).

African Penguins are inshore-foragers and remain resident at their breeding colonies for much of the year. In contrast to penguins which breed in highly seasonal environments, African Penguins breed throughout the year, and frequently lay replacement and second clutches (Cooper 1980, Randall & Randall 1981, Wilson 1985, La Cock *et al.* 1987, Crawford *et al.* 1999, Kemper 2006, Chapter Five), resulting in a prolonged breeding season. However, there still tends to be peaks in breeding activity, which have been attributed to the availability of food in the vicinity of breeding colonies (Randall & Randall 1981, Wilson 1985, Crawford *et al.* 1999). African Penguins moult annually (Randall & Randall 1981, Randall *et al.* 1986); moult is a debilitating process and includes a 21 day period in which the birds are not properly waterproofed and insulated and are thus confined to land (Rand 1960, Randall & Randall 1981). As a consequence they cannot eat and must rely on their fat reserves to sustain them through the fast; this energetically expensive process results in birds losing up to 54% of their body mass (Randall 1989).

The annual cycle of African Penguins has been described for St Croix Island (33°48'S, 25°46'E) in the Eastern Cape (Randall & Randall 1981, Randall 1983), and Robben Island (33°48'S, 18°23'E) in the Western Cape (Crawford *et al.* 1995b). At both colonies, the timing of moult is synchronous, and is thought to be determined by the main breeding season; birds tend to breed when the availability of food close to the colony is

greatest, and are therefore constrained to moult outside of this time (Randall & Randall 1981, Crawford *et al.* 2006a).

The foundering of the *Apollo Sea*, a bulk ore carrier, in June 1994 southwest of Dassen Island at approximately 33°32'S, 17°50'E (Erasmus 1995) resulted in the contamination of about 10 000 African Penguins (Underhill *et al.* 1999). The majority (74%) of these were removed from Dassen Island (33°25'S 18°05'E), the remainder were from Robben Island (25%) and other west coast breeding colonies and the mainland coastline (Dehrmann 1994). Six years later, in June 2000, another bulk ore carrier, the *Treasure* sank about 16km north of Robben Island (Cheney 2000, Crawford *et al.* 2000). The resulting oil spill contaminated about 19 000 African Penguins. An additional 19 500 unoiled penguins were caught at Dassen and Robben Islands and evacuated to Cape Recife (34°02S, 18°30E) in the Eastern Cape, about 800km away, to prevent them from becoming oiled (Crawford *et al.* 2000). The *Apollo Sea* and *Treasure* incidents represent the two worst oils spill events in South Africa in terms of the numbers of seabirds to have been affected (Nel & Whittington 2003). In the year following the *Apollo Sea* spill, moult of adult-plumaged birds at Robben Island was one month earlier than the average moult peak for the island and was also less synchronised (Underhill & Crawford 1999). Moult peaked two weeks earlier in the year following the *Treasure* oil spill at Robben Island (Hemming 2001, Crawford *et al.* 2006a).

The breeding and moult phenology of African Penguins at Dassen Island was studied from December 1994 to March 2006 in order to understand the annual cycle of penguins at the largest breeding colony for the species. The idea that the timing of moult is determined by the timing of breeding activities is reconsidered. An alternative hypothesis, which proposes that the synchrony of moult indicates that this is the priority activity driving the annual cycle, is put forward. The short and medium to long term impacts of the *Apollo Sea* and *Treasure* spills on the patterns of breeding and moult for African Penguins at Dassen Island are also investigated.

METHODS

Study Area

Dassen Island is situated on the west coast of South Africa, approximately 55km north west of Cape Town (Figure 2.1). During the course of this study, Dassen Island supported the largest African Penguin colony (du Toit *et al.* 2004, Hockey *et al.* 2005). The island is divided into nine monitoring and management areas, A–I (Figure 2.2), and penguins breed in all of these areas. The majority (>90%) of penguins nest under cover, in burrows excavated in sand, guano or a shell-guano conglomerate, in clefts between granite boulders and under shrubs; the remainder nest in the open. Distinct colonies can be recognised, and range from high density colonies with nests approximately 1m apart (Hockey & Hallinan 1981) to moderate and low density colonies and also loose groupings of birds.

Breeding Phenology

Details of the flipper-banded birds released following the *Apollo Sea* spill are provided in Chapter Two, and for birds released after the *Treasure* spill in Chapter Six. Burrow occupancy surveys were conducted in five study areas on the island (Figure 2.2). Burrows in Areas B and G were excavated in a sandy substrate; the substrate in Areas A, D and F comprised a shell-guano conglomerate. In order to compare the density of nests within each study area (sub-colony), 30 inter-nest distances were measured per sub-colony from the edge of a burrow to the edge of the closest burrow. Between December 1994 and March 1996, surveys were monthly for Areas B, D, F and G. Between April 1996 and August 2006, surveys took place every two weeks. Surveys were initiated in Area A in May 1997, and were conducted twice a week until August 2006. Within each study area an area comprising c. 200 burrow nests was selected (Figure 2.2); the same area was monitored in each survey. In some surveys it was not possible to complete the census in order to avoid disturbance to other species of surface-nesting birds, usually Cape Cormorants *Phalacrocorax capensis* or Great White Pelicans *Pelecanus onocrotalus*. On some surveys fewer than 200 nests were inspected, and in others additional nests from adjoining sections of the same Area were inspected. No surveys were conducted from June to November 2005. There were other periods in which isolated surveys were missed; these gaps were filled by linear interpolation.

In each survey, all burrow nests within the study area were inspected, and classified into one of the following categories: 1) Burrows with eggs (only those with incubating adults; i.e. abandoned eggs were not included, but were classified as unoccupied – see below); 2) Burrows with chicks; 3) Burrows with pairs (comprising a pair of penguins defending a nest, but without eggs or chicks); 4) Burrows with loafers (individual penguins without eggs or chicks, and not moulting); 5) Burrows with moulters; 6) Unoccupied burrows.

All flipper-banded penguins were recorded during the survey, together with the activities of the re-sighted birds (Table 2.1). Details of the re-sighting methods are provided in Chapter Two. In Areas B and G, the remainder of the monitoring areas (i.e. in addition to the 200 nest survey area) were also searched for flipper banded penguins. The extra search effort for flipper-banded penguins in these areas was due to the larger concentration of de-oiled *Apollo Sea* birds, which were the focus of restoration and breeding success studies (Chapters Two and Five).

Because the dates of the surveys for the five study areas were not the same, the counts of the different categories, as well as the proportions in each survey, were interpolated linearly between counts to estimate the daily numbers and percentages and for each study area (Underhill & Crawford 1999). The daily interpolated percentages for each category were divided into five day periods, or pentades (Berthold 1973). The values at the mid-point of each pentade were used to produce correlation matrices. These were in turn used as the input to an ordination algorithm to calculate co-ordinates that reflect the correlation matrix. The chosen ordination method was non-metric multidimensional scaling (Kruskal 1964a, b) minimizing the "log-stress" objective function (equation 5.3.5 of Greenacre & Underhill (1982), as implemented in the MDS directive of GenStat 8 (GenStat Committee 2005)). This represented, in two dimensions, the differences in breeding patterns between colonies, between categories and between years. For example, if the pattern of egg-laying in two colonies or years was exactly the same, the distance between these two co-ordinates on the plot produced by the multidimensional scaling algorithm would be zero. Plotted co-ordinates conceptually illustrate the differences between colonies, years and categories (Greenacre & Underhill 1982).

Information from the Dassen Island re-sighting database (see Chapter Two) was used to describe the pattern of breeding for penguins that were oiled in the *Apollo Sea* oil spill in June 1994 (Underhill *et al.* 1999), and those that were oiled and evacuated following the *Treasure* oil spill in June 2000 (Crawford *et al.* 2000), and to compare the pattern of breeding of these individuals with the colony in which they bred. Comparisons were possible for *Apollo Sea* birds in Areas B and G, and for *Treasure* birds, in Areas B, F and G. The small numbers of *Apollo Sea* and *Treasure* birds in the other study areas (Areas A and D) precluded accurate comparisons.

Moult Phenology

Counts of penguins in the feather-shedding phase of moult were conducted at weekly intervals from the end of November 1994 until July 1999, and at two-weekly intervals from August 1999 until September 2006. Adult and juvenile moulters were counted separately. The counts were made along the coast, where the majority of birds congregate to moult, and were conducted separately for each coastal monitoring area (A–G; Figure 2.2). Penguins also moult within breeding colonies. All moulting birds observed in the colony from the coast were included in the total. The burrow occupancy surveys provided an indication of the proportion of burrows that contain moulters at different times of the year, but these figures were kept separate from the moult count totals because individual moulters do move between the colonies (and nest sites) and the coast. During the moult counts, re-sightings of flipper-banded birds were made using a spotting scope, and the information was incorporated into the Dassen Island re-sighting database.

Following Underhill & Crawford (1999), counts of moulting penguins were interpolated linearly to fill gaps in the data and to estimate the numbers of birds moulting each day. The interpolated figures were summed for each week. Week 1 was defined as the week beginning 1 July (Appendix 3.1). Thus the year spans the period July to June. This split of the year is appropriate because the moult peak for Dassen Island takes place over the period October to January and numbers of moulters are smallest in June/July. The summed amounts for each week represent the number of moult-days per week, and not the number of individual moulters. The feather-shedding period of moult lasts on average 12.7 days (Randall *et al.* 1986). The number of moult-days per week was therefore divided by 12.7 to estimate the number of birds reaching the mid-point of moult

in each week. The number of birds reaching the mid-point of moult in each month was also calculated in this manner. The average annual pattern of moult for birds moulting along the coast (i.e. excluding birds moulting in burrows) was obtained by adding the estimated number of birds reaching the mid-point of moult in each week over all years, and expressing this figure as the percentage of birds that moulted in each week (Week 1–52).

Re-sighting information was used to determine the pattern of moult for penguins involved in the *Apollo Sea* and *Treasure* oil spills. The moult patterns of these birds were compared with the moult cycle of all penguins on Dassen Island, and also to un-oiled flipper-banded penguins. For each month from December 1994 to June 2000 the ratio of *Apollo Sea* moulters to un-oiled flipper banded moulters was calculated.

Intervals between moults and between moult and breeding

For flipper-banded penguins that were observed moulting, five phases of moult were recorded: 1) Pre feather-shedding (fattened birds just about to loose their first feathers); 2) Beginning of the feather-shedding phase (birds dropping their first feathers); 3) Full feather-shedding phase (in the process of shedding feathers); 4) End of the feather-shedding phase (only a few feathers left to shed) and 5) Post feather-shedding phase (shed all feathers, with evidence of old feather sheaths still clinging to the body). For birds that were not observed in the "middle" of the feather-shedding period (i.e. phases 1, 2, 4 and 5), the date on which they were observed moulting was used to estimate the date on which the mid-point of feather-shedding would fall using the method developed by Kemper & Roux (2005): a) Ten days were added for birds in pre feather-shedding condition (6.1% of moult re-sightings); b) Six days were added for birds that were observed at the beginning of the feather-shedding period (0.33%); c) Birds in full feather-shedding phase were assumed to be at the middle of their moult, and no days were added or subtracted (70.7%); d) Six days were subtracted for birds that were observed at the end of the feather-shedding period (10.26%); e) Ten days were subtracted for birds in post feather-shedding condition (9.36%). The estimated mid-point of moult was used to calculate the intervals between successive moults.

The interval between the completion of breeding activities and the mid-point of moult was calculated by investigating the re-sighting database. This analysis was restricted to

Areas B and G, which received more regular and thorough re-sighting effort, and where cohorts of nests were monitored to determine breeding success (Chapter Five). For monitored nests, the date on which the bird completed its breeding attempt (when the fledged chick left the nest or the adults abandoned the nest) was known to within five days (the interval between nest checks). For birds that were not monitored in study nests, the last occasion the bird was re-sighted breeding (either incubating eggs, or brooding or guarding chicks) was taken as the date it completed its breeding activities.

To determine the interval between moult and the first breeding attempt thereafter, the estimated date of egg-laying was calculated. For birds in breeding study nests, the egg-laying date was back-calculated from the hatching date (Chapter Five). For birds that were not monitored in study nests, the first breeding re-sighting within a year of the moult date was used. Breeding activities recorded for re-sightings in this study include "Eggs", "Downy Chicks" and "Blue Chicks" (Table 2.1). Chicks were recorded as "Downy" if they had lost less than half of their down, and as "Blues" if they had lost more than half of their down. The mean incubation period for African Penguins is 38 days (Williams & Cooper 1984). Chicks first start loosing their down from about 35 days of age (Seddon & van Heezik 1993, ACW unpubl. data), and were generally about 45 days old by the time they lost half of their down (unpubl. data). Birds re-sighted with eggs were assumed to be halfway through incubation, and so 19 days were subtracted from the re-sighting date. For birds first re-sighted with "Downy Chicks" and "Blue Chicks" 40 days and 70 days were subtracted from the re-sighting date, respectively. In this way, the egg-laying date was estimated and the interval between moult and the egg-laying date was calculated.

RESULTS

Breeding phenology and patterns of burrow occupancy

The inter-nest distances in Areas A, D and F were shorter than those in Areas B and G (Table 3.1). Consequently, the sub-colonies in Areas A, D and F were termed high-density colonies and those in Areas B and G, moderate density colonies. In all five study areas, birds were recorded with eggs and chicks in every month of the study (Figure 3.1). There were usually several breeding peaks per year. The pattern of breeding was

not consistent from one year to the next (Figures 3.1 & 3.2). However, there was a tendency for breeding activities, especially egg-laying, to decline from August until November in Areas A, D and F, but not in all years (Figure 3.1). This was also the case in Areas B and G from 2001–2004. The percentage of burrows with eggs in the five study areas fluctuated in a broadly similar pattern; the strongest similarities were between Areas A, D and F, and between Areas B and G (Figure 3.3). There were only five surveys, out of 1 059 conducted, in which none of the burrows inspected contained eggs. These were in Area F in the beginning of June 2006 and in Area A in early and late November 1999 and mid to late October 2000. In other surveys in Area A and Area F in these months, eggs were recorded, hence the earlier finding that eggs were found in every month of the study. The percentage of burrows with birds incubating eggs ranged from zero in the five surveys referred to above, to 56.2% for Area B in early January 1995. Similarly the percentage of burrows containing chicks ranged from zero, in Area A in late November 2004, to 55.2%, also in Area A, in early May 2000.

The overall percentage of burrows that were unoccupied during the course of the study differed significantly between study areas (Kruskal-Wallis $H = 86.51$, df = 4, $P < 0.001$). The area with the largest mean percentage of burrows unoccupied was Area A, followed by Area D; Area G had the smallest mean percentage of empty burrows (Table 3.2). The largest recorded percentage of unoccupied burrows was 96.6% in Area A in early December 1999 (Figure 3.2).

The number and percentage of burrows with adult moulters varied considerably in extent during the course of this study (Figure 3.2). In many (26%) of the surveys no moulting birds were detected. The maximum percentage of burrows with adult moulters ranged from 17.7% in Area B in September 1995 to 35% in Area F in September 2001. The pattern of adult penguins moulting in burrows was strongly seasonal and synchronous, especially in Areas A, D and F (Figure 3.4). The peak in burrow moulting occurred from Week 10 (beginning of September) to Week 19 (beginning of November) (Figure 3.4). The frequency of re-sightings of flipper-banded penguins moulting in burrows peaked from June until October; the largest numbers of re-sightings were made in August and September (Figure 3.5a). This pattern was different to the distribution of flipper-banded penguins moulting along the coast, which peaked from October–December (Figure 3.5b).

The plot produced by non-metric multidimensional scaling using the correlation matrix derived from the percentages of burrows with different activities for all study areas and for all years shows the co-ordinates for Area G eggs and Area B eggs clustered; points for Area D eggs and Area F eggs were also clustered, but away from Area G and B (Figure 3.6). The points for burrows with chicks were plotted close together for Areas D, F and G, with Area B separate from the other three areas. The points for burrows with moulters were placed well apart from the points for eggs and chicks, and for all four areas were tightly clustered, more so than the points for burrows with eggs or chicks (Figure 3.6). The percentages of nests with pairs, loafers and of unoccupied nests were placed further apart than was the case for eggs, chicks and moult (Figure 3.6).

When plotting points for burrows with eggs and moulters separately for each area, it is clear that there are differences between areas in the inter-annual patterns of these two activities in burrows (Figure 3.7). The positions of the points for moult in each area were located on the negative side of the x-axis, except for moult in Area B in 1997 and 1998. The points for eggs were mostly on the positive side of the x-axis, with exceptions in Areas B (1996, 1997 and 1998) and G (1996 and 1997). In all areas, the points for moult tended to be more clustered than the points for eggs. In Area G, the points for moult were distributed in two clusters, one which included the years 1995–1998, and the other for years 1999–2004 (Figure 3.7e). In Area F 1997 and 2001 were separated from other years for moult (Figure 3.7d). In September 2001 a much larger percentage (35%) of burrows contained moulters than in other years. Areas A, D and F showed tighter clustering of points for both eggs and moulters than Areas B and G. Points for Area B were the most widely scattered of all areas for both eggs and moulters.

Breeding phenology of birds involved in the *Apollo Sea* and *Treasure* oil spills

De-oiled penguins from the *Apollo Sea* oil spill were released from 26 July 1994 until 11 September 1994 (Underhill *et al.* 1999). In the first month of post-release monitoring at Dassen Island (September 1994) 13 de-oiled penguins were recorded breeding. By the end of December 1994 306 *Apollo Sea* birds had been recorded breeding, 110 in Area B and 155 in Area G (see Figure 2.6). The first major peaks in egg-laying by de-oiled *Apollo Sea* birds were in April and May 1995 for Area G and Area B, respectively (Figure 3.8). From January 1995 until December 2004, the pattern of breeding of de-oiled *Apollo*

Sea birds, expressed as the number of birds incubating eggs, was similar to the rest of the colony in which the birds bred (measured as the percentage of burrows with incubating adults), for both Areas B and G (Figure 3.8, Table 3.3).

Following the foundering of the *Treasure* in June 2000, a total of 12 345 un-oiled African Penguins were evacuated from Dassen Island in early July 2000 and transported to Cape Recife (34°02'S, 18°30'E), near Port Elizabeth (Crawford *et al.* 2000, Chapter Six). Eight of these birds were recorded incubating eggs at Dassen Island on 18 July 2000, five birds in Area B and three in Area G. It is likely that in at least some of these cases the mate of the evacuated birds must have continued incubating the eggs in the absence of the evacuated bird. Penguin S21227 was evacuated from Dassen Island on 3 July 2000. It was first observed back at Dassen Island on 18 July incubating two eggs in Area B. On 24 July and 4 August, S21227 was recorded brooding two downy-chicks. Given the mean incubation period for African Penguins of 38 days (Williams & Cooper 1984), it is evident that the eggs were laid before S21227 was evacuated from Dassen Island, and that its mate had continued incubating the eggs in its absence. There were no further observations of S21227 until 3 November 2000, when it was recorded moulting in a burrow in Area B. The *Treasure*-evacuated birds showed an initial peak in egg-laying in August 2000, one month after the birds were evacuated from Dassen Island in both Area B and Area G (Figures 3.9a,c). This was followed by a larger peak in November (Area B) and December (Area G), and, in both areas, a substantially larger peak in May 2001 (Figures 3.9a,c). Of the three study areas, Area F had the lowest number of evacuated birds. These birds showed a small peak in egg-laying in January 2001, and a larger peak in May–June 2001 (Figure 3.9b). In all three areas, the pattern of incubation for *Treasure* evacuees over the entire duration of the study (July 2000–December 2004) was similar to that of the colony in which the birds bred (Figure 3.9, Table 3.3).

One de-oiled *Treasure* bird was recorded breeding on 23 August 2000. None were recorded breeding in October 2000, and by the end of December 2000, 23 had been recorded breeding. Relatively few de-oiled *Treasure* birds bred in Areas B and G compared with Area F. In both Areas B and G, the first peak in egg-laying for de-oiled *Treasure* birds was in May 2001; in Area F there was a peak in January 2001, followed by a larger peak in May 2001 (Figure 3.9). The pattern of egg-laying for de-oiled

Treasure birds was comparable with that of the colony in which the birds bred for all three areas (Figure 3.9, Table 3.3).

Pattern of moult

The proportion of African Penguins in adult plumage that moulted along the coast peaked from Week 20–Week 23 (Figure 3.10), which comprised the period 11 November – 8 December (Appendix 3.1). By the end of Week 23, 54% of the adult-plumaged birds had moulted. Seventy-five percent of adults had moulted by the end of Week 27 (ending 5 January). The seasonal pattern was similar for all coastal monitoring areas (Figure 3.11).

A total of 39 de-oiled penguins from the *Apollo Sea* spill was recorded moulting between August 1994 and the end of December 1994; 22 of these were recorded in December. The re-sighting effort was low in the period September–November 1994. It increased in December, and remained relatively constant until the end of 2002, when it became more erratic. In 1995, numbers of de-oiled *Apollo Sea* adults moulting peaked in June and again in September (Figure 3.12), in contrast to the seasonal pattern for all adult-plumaged birds, which peaked in November–December (Figure 3.10). The pattern of moult of *Apollo Sea* birds in 1995 also differed from that of un-oiled flipper-banded birds in adult plumage (the control group), which largely conformed to the average seasonal pattern for all birds (Figure 3.12). From June to September 1995, when the total number of birds moulting was low, the number of *Apollo Sea* birds moulting was between 15 and 42 times the number of control birds moulting (Figure 3.13). The following year, the distribution of moulting de-oiled *Apollo Sea* birds was again bimodal, with a minor peak in May 1996, and a much larger peak in October 1996. Although the number of control group moulters peaked in November 1996, the patterns of moult for the two groups were more synchronised than the year before, and became well synchronised thereafter (Figure 3.12). The ratio of *Apollo Sea* to control bird moulters generally remained above one between October 1995 and June 2000, which was largely a reflection of the larger number of *Apollo Sea* birds compared to un-oiled flipper-banded birds at the Dassen Island colony. However, the ratio was always substantially lower than the peak of June to September 1995 (Figure 3.13). The patterns of moult for the *Apollo Sea* and control birds were not correlated for the period December 1995–July 1996 (r_s = –0.011, df = 18,

$P = 0.96$), but were correlated from August 1996–July 2000 ($r_s = 0.73$, df = 46, $P < 0.001$).

Four de-oiled birds from the *Treasure* spill were recorded moulting in August 2000, one month after the first de-oiled birds were released. The number of de-oiled *Treasure* birds moulting peaked in November 2000, at the same time as the count for all adult-plumaged penguins moulting along the coast (Figure 3.14). The patterns remained similar for the duration of the study: August 2000–December 2004 (Figure 3.14). The number of *Treasure* evacuated birds moulting peaked in February 2001. There were also minor peaks in November 2000 and April–May 2001. The moult peak for *Treasure* evacuees was less synchronised (broader) than for de-oiled birds, especially in the first year after the spill (Figure 3.15). In the following year, the moult peak for *Treasure* evacuees was closer to that of the de-oiled *Treasure* birds, and was more synchronous, but during this year and all the following years, there were differences in the timing of moult peaks between these two groups of birds (Figure 3.15). The number of *Treasure* birds recorded moulting after 2001 was relatively small, especially for *Treasure* evacuees, making rigorous comparisons for this period difficult. The small sample sizes after 2001 were largely due to a reduction in re-sighting effort.

Moult intervals

A total of 2 837 flipper-banded penguins in adult plumage were observed moulting during the course of the study. The number of individuals for which successive moults were recorded was 478, and the number of moult interval records was 701. The interval between successive moults ranged from 221 days to 546 days (Figure 3.16). The mean moult interval for all birds and all years was 349 days (SD = 44.0 days, $n = 701$). There was no difference between the moult intervals of de-oiled *Apollo Sea* birds and other flipper-banded birds (Mann-Whitney $U = 171\,000$, $n_1 = 711$, $n_2 = 487$, $P = 0.72$). The median moult intervals differed significantly between years (Kruskal-Wallis $H = 24.88$, df = 9, $P = 0.003$). The shortest moult intervals were recorded in the periods 2002–2003 and 2003–2004, and the longest in 1998–1999 and 2000–2001 (Table 3.4). Birds with moult intervals less than 280 days were recorded in every interval period, except for the period 1994–1995, when there were only two moult interval records (Table 3.5). The period with the highest frequency of short intervals, standardised for the number of moult interval records per period, was 2002–2003. Fifty-seven birds were recorded moulting in

more than two consecutive years (Table 3.6). Penguin S20882 was recorded moulting in six consecutive years, from 1995 until 2001. The mean moult interval for S20882 was 365.2 days (SD = 36.11, n = 6), with a range from 317 days in the period 1995–1996 to 421 days in the 2000–2001 period. The interval of 421 days was 13% longer than the next longest interval of S20882. Re-sighting records show that on 22 March 2001, S20882 was brooding two downy chicks in a burrow in Area G, 311 days after its previous moult. There were no further re-sightings of this bird until 26 June 2001, when it was observed loafing along the coast in Area G. It was recorded moulting on the coast of Area G 14 days later on 10 July 2001. It is not known whether S20882 continued rearing the chicks after 22 March 2001 and for how long. Re-sightings of adults after the "guard stage" are much scarcer than for birds brooding downy chicks because both parents then forage during the day at sea and spend less time in the colony. If the chicks were successfully fledged, they would have required at least another 40 days at the nest. S20886 would also have required a pre-moult fattening period at sea of approximately 30–40 days before moult (Randall & Randall 1981).

Intervals between breeding and moult

The observed interval between the completion of a breeding attempt and moult was significantly less for birds monitored in breeding success study nests (median = 86 days) than for non-study birds (median = 123 days) (Mann-Whitney U = 102 400, n_1 = 254, n_2 = 1161, $P < 0.001$).This difference was likely due to the completion of breeding being inaccurately estimated for non-study birds. Further analyses and results were therefore restricted to birds that were monitored in study nests. For these birds the mean interval between the completion of a breeding attempt and the next moult was 97.7 days (SD = 58.6, n = 254), and ranged between seven and 342 days (Table 3.7). The breed to moult interval did not differ significantly between years (Kruskal-Wallis H = 9.64, df = 5, P = 0.09, Table 3.7). The mean interval between the mid-point of moult and the estimated egg-laying date was 102.8 days (SD = 61.6, n = 1 590), and ranged from 29 to 360 days. The moult to breed interval differed significantly between years (Kruskal-Wallis H = 58.96, df = 9, $P < 0.001$, Table 3.8). The shortest intervals were recorded in 1999 and 2003, and the longest in 1995 and 2004 (Table 3.8).

Location of moult

Of the 4 121 re-sightings of flipper-banded penguins moulting, 2 816 (68.3%) were of birds moulting on beaches, 1 233 (30%) were of birds moulting in nest sites and 72 (1.7%) comprised birds moulting outside of nests in breeding colonies. The monthly distribution of re-sightings was different for birds moulting along the coast and in nest sites; moulters were re-sighted in burrows more frequently from June to October, and on the coast from October to December (Figure 3.5). Of the 701 consecutive moults recorded for 478 individuals, 512 (73%) were consistent from one moult to the next in terms of whether the bird moulted in a nest or on the coast, the remaining 189 (27%) records representing birds that moulted on the coast or beach in one year and changed the following year. These changes tended to conform to the pattern of re-sightings for birds moulting in burrows and on the coast, the bird being more likely to moult in a burrow from June to September, and on the coast from October to January (Figure 3.5). For example, Penguin S24931 was recorded moulting in a nest site in 1995, 1996 and 1998. On each of these occasions it moulted in August. In 1999, S24931 moulted in December, and on this occasion it moulted on the coast. A total of 38 birds were recorded moulting both on the coast and in a nest on separate days during the course of one moult.

Individuals seldom moulted in more than one of the monitoring areas (see Figure 2.2) during the course of the study. Of the consecutive moult intervals recorded, 674 (96.2%) were of birds that moulted in the same area. Similarly, birds tended to moult in the area in which they bred. Excluding records for birds that bred in Areas H and I, which do not include any coastline (Figure 2.2), 890 (96.5%) of the records were of birds moulting and breeding in the same monitoring area. Birds that bred in Area H and moulted on the coast tended to moult in Area G (82.6%). Breeders from Area I were recorded moulting in Areas A (45.5%), B (27.3%), G (18.2%) and D (9.1%). Fifty-two moult records were of flipper-banded birds moulting in the nest site at which they bred, including seven where the breeding pair was moulting together. The incidence of birds moulting at their own nest sites is likely to be much greater than reported here. The numbered nest markers were mostly removed soon after the completion of the breeding attempt so that new markers could be deployed for the next cohort of study nests (see Chapter Five). Consequently, most of the nests in which birds moulted were not marked, making it difficult to determine whether it was the same nest in which the bird bred.

DISCUSSION

Breeding phenology of African Penguins at Dassen Island

Timing of breeding and moult in seabirds typically correspond to patterns of favourable environmental conditions, such as food supply (Lack 1968, Perrins 1970). Breeding activities are generally timed so that peak availability of food in the vicinity of the breeding colony occurs during the energetically-demanding chick-rearing period (Davis & Cuthbert 2001). Food availability prior to breeding can also be a limiting factor; body mass of Magellanic Penguins *Spheniscus magellanicus* at the onset of incubation has been found to be the most important determinant of nest desertions (Yorio & Boersma 1994). Humboldt Penguins at Punta San Juan (15°22'S, 75°12'W) in Peru appear to moult, rather than breed, during the period of peak food availability (Paredes *et al.* 2002). Timing of breeding and moult are probably most critical for penguins breeding at moderate to high latitudes, where seasonality is more pronounced. These species have relatively distinct periods in which the availability of food and physical conditions, such as the extent of sea-ice in the case of Antarctic penguins, are favourable (Croxall & Davis 1999).

African Penguins are typical inshore foragers, feeding relatively close to the colony during breeding, and generally remaining resident for a large part of the year (Croxall & Davis 1999, Petersen *et al.* 2006). They have a complex annual cycle, characterised by a prolonged breeding season, which is due mostly to their ability to lay replacement and second clutches, i.e. those laid after a successful breeding attempt (Cooper 1980, Randall & Randall 1981, Crawford *et al.* 1995a, b, 1999, Chapter Five).

The almost continuous breeding of African Penguins during this study suggests that food was available for a large part of the study period. There were distinct peaks in breeding activity, but the timing of these varied between years and colonies. It is therefore difficult to quantify an average seasonal pattern of breeding for penguins at Dassen Island. There was however a tendency for breeding activities to tail off from August to November, although this was not always the case; in some years and at some colonies, breeding activities peaked in these months. Reduction in breeding activities from August to November coincided with the peak moult period at Dassen Island during the study. In contrast to African Penguins at Stony Point (Whittington *et al.* 1996), Robben Island

(Crawford & Boonstra 1994, Crawford *et al.* 1995b), Malgas Island (33°03'S, 17°55'E) (Crawford *et al.* 1995a) and Marcus Island (33°02'S, 17°58'E) (La Cock *et al.* 1987), where breeding activities almost ceased during the peak moult period, there was considerable overlap of moult and breeding at Dassen Island. Cooper (1980) reported two egg-laying peaks for African Penguins at Dassen Island during the period 1971–1972, one in June and the other in November–December. During the same period, numbers of penguins moulting at Dassen Island peaked in October and August in 1971 and 1972, respectively (Cooper 1978), suggesting a separation of peak moult and breeding activities. However, a closer examination of these results reveals a degree of overlap in breeding and moult, especially in October and November.

Although there was no clear overall seasonal pattern to the breeding activities at Dassen Island, there were broad similarities between areas and varying degrees of synchronisation within areas, albeit at a low level. If there was no synchronisation in breeding activities, birds of all stages of breeding would be found in roughly equal proportions throughout the year (Seddon *et al.* 1991). This was not the case, with peaks in egg-laying observed in all of the areas. Areas B and G were the two areas with the most irregular pattern of breeding. Areas A, D and F, showed greater levels of synchronisation both within the colonies and between them. The greater degree of synchronisation in these areas is probably related to the higher density of nests than in Areas B and G. African Penguins engage in a range of behavioural and vocal displays during pair formation and breeding (Eggleton & Siegfried 1979), which may stimulate breeding activities of other birds in the immediate vicinity and thereby facilitate increased synchrony in high-density colonies (Waas 1988, 1995, Seddon *et al.* 1991, Waas *et al.* 2000).

Greater synchronisation of breeding activities between individuals in close proximity than those that are further apart has been shown for a number of colonial seabird species (Murphy & Schauer 1996, Mougin *et al.* 2001). Local-scale synchrony resulting from social interaction has been reported for Galápagos Penguins (Boersma 1976). African Penguins at St. Croix Island showed greater synchrony within colonies than for the island as a whole (Randall & Randall 1981). The degree of synchrony varied between colonies, with 23 marked pairs in one colony completing egg-laying within nine and 14 days in two successive years. This degree of synchrony is far greater than was the case

for any of the colonies at Dassen Island. Randall & Randall (1981) did not report whether differences in breeding synchrony were related to nest density. Seddon *et al.* (1991) reported a low level of hatching synchrony at three low density colonies of African Penguins on Dassen Island in the late 1980s, and indicated that local synchronisation, rather than a wider-scale seasonal effect, was responsible for the observed breeding phenology.

Another factor which likely contributed to the prolonged and irregular nature of the breeding season was the incidence of replacement and second clutches. From 1994–2000, 60% of birds that were observed breeding again after a monitored breeding attempt laid their second clutch within five months of successfully completing the previous attempt (i.e. where chicks fledged). Sixty percent of birds that failed during the incubation stage and 54% of birds that failed at the chick stage laid replacement clutches within five months of the previous attempt having failed (Chapter Five). The median interval between the completion of the previous breeding attempt (including both successful and failed attempts) and the initiation of the following breeding attempt ranged between 4.4 months for birds which failed during the incubation stage and 5.3 months for birds which failed at the brood stage (Chapter Five). The colony showing the least synchronous pattern of breeding was Area B. Breeding success in Area B was consistently lower than in Area G (Chapter Five). It is unclear if these two findings are related, and if so, how. Higher levels of nest failure may result in an increased frequency of replacement clutches being laid thus contributing to erratic patterns of egg-laying. On the other hand, lack of synchrony within the colony may have contributed towards reduced breeding success (Coulson 2002). Other factors which influence reproductive success will also influence the incidence and pattern of replacement clutches and therefore the overall breeding phenology observed in a colony. Some of these factors vary seasonally. For example, although African Penguins tend to breed more successfully in burrow nests than in open nests (Frost *et al.* 1976a); nests which are made in a shell-guano substrate flood more frequently than burrows in a sandy substrate during the austral winter rains, reducing chick survival during this time (La Cock 1988, Seddon & van Heezik 1991). Unused burrows in the shell-guano conglomerate tend to remain unoccupied without collapsing for longer than burrows in sandy soil, which probably accounts for the higher overall percentage of unoccupied burrows in Areas A and D (both areas with nests in shell-guano substrate).

Previous studies of African Penguins have provided support for Lack's (1968) hypothesis that birds time their breeding so that the peak food availability occurs during chick-rearing in order to maximise chick growth rates and minimise chick mortality. Randall & Randall (1981) ascribed the peak in breeding activities of African Penguins at St. Croix island to the annual abundance of Sardine *Sardinops sagax* in the area from April to June. A west coast breeding peak in the austral winter (May–September) has been attributed to the abundance of post-larval Anchovy *Engraulis encrasicolus* off the west coast of southern Africa from April–September (Crawford 1981, Duffy *et al.* 1984, Wilson 1985, Crawford *et al.* 1995a, 1999). Wilson (1985) found that most penguins at Marcus Island bred during the period in which chick growth rates were highest, and chick mortality was lowest, and suggested that those penguins breeding at non-optimal periods (when chick growth and survival were lowest, from September to February) may be failed breeders laying replacement clutches or immigrants from other colonies with different annual cycles. Wilson's (1985) study took place over a period of only one year, from June 1980 to July 1981. From 1994–2000 breeding success of African Penguins at Dassen Island was found to be markedly higher than previous estimates, with no significant seasonal effect (Chapter Five). Further, while the standardised growth rates of chicks varied over time, the pattern differed between years, suggesting that fine-scale periods of improved food availability were not seasonally predictable (Figure 3.17). The annual fledging success of African Penguins at Dassen Island between 1995 and 1999 was, however, significantly related to the spawner biomass of Anchovy and Sardine (Chapter Five, Figure 5.3).

Off South Africa, Anchovy and Sardine are the main prey of African Penguins (Hockey *et al.* 2005). Regional trends in the populations of African Penguins have been related to changes in the abundance and distribution of Anchovy and Sardine, and changing patterns of dominance of these two species, termed regimes (Lluch-Belda *et al.* 1989, Crawford 1998). Sardine was the dominant prey species in the Benguela system off South Africa up until the mid 1960s. Anchovy then became dominant until the mid to late 1980s, when the system reverted back to one of Sardine dominance (Crawford 1998, 1999). Penguin colonies between Lüderitz and Table Bay are thought to benefit from a system dominated by Sardine. This is because, in addition to the young fish that recruit to the nursery grounds along the west coast north of Table Bay in the austral autumn

and winter, older fish are also available north of Table Bay (Armstrong *et al.* 1987, Crawford 1998), resulting in a longer period of reliable food availability. In an Anchovy dominated system, older fish tend to remain on the western and central Agulhas Bank, out of reach of breeding penguins at colonies north of Table Bay (Crawford 1998). The only consistently available fish to penguins at these colonies in such a system are the post-larval fish which are transported by currents to the nursery areas along the west coast, and the later migration of young-of-the year fish southwards to the Agulhas Bank (Crawford 1980, 1998).

Between the mid 1990s and 2001 there was a rapid increase in the biomass of both Anchovy and Sardine off South Africa (Barange *et al.* 2004); the combined spawner biomass of Anchovy and Sardine in 2001 was double any previous estimates obtained by means of a direct survey (Crawford *et al.* 2001a, van der Lingen *et al.* 2001). The increased abundance of fish translated into a 14% increase in the number of African Penguin breeding pairs in South Africa between 2000 and 2001 despite the loss of about 2 000 penguins during the *Treasure* oil spill in June 2000 (Wolfaardt *et al.* 2001). After 2002 there was a reduced availability of food to African Penguins on the west coast due to the eastward shift in the distribution of Sardine, but most of the period included in this study (especially from 1995–2002) can be characterised as one in which pelagic fish was relatively abundant and more consistently available for a longer part of the year compared to the period of at least 30 years prior to the study (van der Lingen *et al.* 2005, Fairweather *et al.* 2006, Crawford *et al.* in prep., Chapter Four). In light of this, the almost continuous breeding activity, high frequency of replacement and second clutches and lack of seasonality displayed by breeding African Penguins at Dassen Island is likely to be a result of their capacity to be flexible in response to changing ecological constraints. The adaptive value of this flexibility in a productive but unpredictable environment is that birds are able to maximise their reproductive output during favourable conditions (as during this study), thereby offsetting breeding abstinence and lower productivity during periods of food scarcity (Wilson 1985, Adams *et al.* 1992, Crawford *et al.* 1999), and maximising lifetime reproductive success. This strategy is also a feature of Humboldt (Paredes *et al.* 2002) and Galápagos (Boersma 1976) Penguins, both of which are inshore-foragers that are susceptible to localised changes in environmental conditions.

Breeding patterns of birds affected by the *Apollo Sea* and *Treasure* oil spills

Although some de-oiled *Apollo Sea* birds commenced breeding soon after their release from the rehabilitation centre, the first peak in egg-laying occurred in April–May 1995, about eight to nine months after their release. The lag between the post-release arrival of de-oiled birds at Dassen Island and their first breeding attempt was approximately 11 months (Chapter Two). This lag may have been due to sub-lethal impacts of the oil contamination suppressing breeding activities temporarily (Butler *et al.* 1988, Walton *et al.* 1997), and/or to the loss of a mate and the need to re-establish pair bonds (Chapter Five), or by the annual cycles of an established pair becoming unsynchronised as a result of the rehabilitation process (Fry *et al.* 1986, Kerley & Erasmus 1987, Giese *et al.* 2000). The April–May 1995 peak coincided with an egg-laying peak for the areas in which these birds bred, and the patterns of breeding for de-oiled *Apollo Sea* birds and the colony as a whole were similar throughout the study period, for both Areas B and G. This suggests that the de-oiled birds conformed to the breeding pattern of the areas in which they bred. It is possible that the number and density of de-oiled birds in Areas B and G was sufficient to influence the breeding activities of non-oiled birds in these areas, and that this in turn contributed towards the different and less synchronous pattern of breeding in these two areas compared with the other three study areas. It seems unlikely, though, that this effect would have persisted for more than a couple of years, especially if it resulted in birds breeding during sub-optimal periods; the lower density of nests in these areas is more likely to account for the less synchronous pattern of breeding.

Oil contamination and the rehabilitation process had a similar effect on the breeding patterns of de-oiled *Treasure* birds: an initial delay of about 10 months before the first peak in breeding activities, followed by a pattern of breeding that was comparable to that of the colony in which the birds bred. In contrast, penguins that were evacuated following the *Treasure* spill did not experience the same lag and many commenced breeding soon after they returned to Dassen Island. The shorter lag between the return of the evacuated birds and their first breeding attempts is likely to be due to the shorter period that the birds were away from the colony – two to three weeks in the case of the evacuated birds as opposed to an average of six weeks for the de-oiled birds (Wolfaardt *et al.* 2001) – and possible sub-lethal impacts of oil contamination which may have suppressed breeding activities of de-oiled birds in the short-term (Fry *et al.* 1986, Butler

et al. 1988, Walton *et al.* 1997, Giese *et al.* 2000). Even though the breeding season was protracted and not highly synchronous, all groups of birds involved in oil spills conformed to the colony pattern of breeding, suggesting that in spite of short-term disruptions to breeding activities, the affected birds were able to re-integrate their cycles with that of the colonies in which they bred. This is likely the result of social interaction between birds within a colony facilitating local-level synchrony (Boersma 1976, Gochfeld 1980a, b).

Moult phenology of African Penguins at Dassen Island

In contrast to the breeding patterns, the pattern of moult for African Penguins at Dassen Island was synchronous and seasonal. Most adult penguins moulted between September and January, consistent with results from previous studies on African Penguins from the Western Cape (Cooper 1978, Wilson 1985, Crawford *et al.* 1995b, 2006a, Underhill & Crawford 1999, Hemming 2001). Counts of adult moulters along the coast at Dassen Island peaked in November and December.

Previous studies of moult phenology in African Penguins have generally focussed on birds moulting on "landing beaches" along the coast, because it was thought that few birds moult away from the shoreline (Randall *et al.* 1986, Crawford & Boonstra 1994, Underhill & Crawford 1999). It is evident from this study that, at Dassen Island, a substantial number of birds moulted away from the shoreline, in burrows and at other nest sites. Birds moulting in burrows tended to moult earlier (from June until October, peaking in September and October) than birds moulting along the coast. The shift from moulting in burrows in the austral winter and spring to moulting along the shoreline in summer appears to be related to seasonal climatic variables. During winter and spring, rough sea conditions occur frequently, associated with the cold fronts passing the Western Cape (Wolfaardt 1999). Increased wave action forces penguins on the landing beaches to move up the beach and into the breeding colonies (pers. obs). It would therefore be less disruptive for penguins to moult at nest sites and in the colony during these periods. At Dassen Island ambient temperatures and solar radiation are highest during summer (Figure 1.4). Burrow nests provide a major advantage over surface nests, especially during summer, as they provide incubating birds and chicks a level of protection from high levels of solar radiation, thereby reducing the effects of heat stress (Frost *et al.* 1976a, b, Williams & Cooper 1984, La Cock 1988). The higher incidence of

moulting outside of burrows, along the coast during summer suggests that the sea breezes experienced along the shoreline moderate the high ambient temperatures, making the coastline a more favourable moult locality than burrows at this time. The moderating effect of sea-breezes would not be as beneficial to those penguins moulting away from the coast (i.e. in burrows in the breeding colonies), hence the higher incidence of burrow nesting (as opposed to surface-nesting) during summer (La Cock 1988). Although the plumage of moulting penguins is not properly waterproofed and insulated, they may enter the sea briefly to drink and preen (Cooper 1978, A.C.W. pers. obs.), which would be easier for penguins moulting along the coast. Although this would provide some additional benefit for those penguins moulting along the shore, it is done only infrequently (pers. obs) and so is unlikely to account directly for the shoreline moulting behaviour of penguins during summer.

The much higher level of synchrony and seasonality of moult compared to breeding patterns for African Penguins at Dassen Island is consistent with studies of African Penguins elsewhere, both in South Africa and Namibia (Randall & Randall 1981, Randall 1983, 1989, Wilson 1985, Underhill & Crawford 1999, Hemming 2001, Crawford *et al.* 2006a), and suggests that there are strong environmental or biological variables governing the timing of moult. The timing of moult appears to be related, at least partly, to the African Penguin's protracted breeding "season". Crawford *et al.* (2006a) suggested that the availability of food close to the breeding colony determines the main period of breeding, which in turn dictates the timing of moult for adult African Penguins.

During this study, the almost continuous breeding activity (and lack of distinct seasonality) was attributed to the relatively constant and favourable availability of food. The timing of moult for African Penguins at Dassen Island (and other colonies) appears to be critical to survival; most penguins moult from September to January regardless of any breeding preferences. This might suggest that foraging during the pre-moult fattening period is influenced by factors independent of the breeding period, and that birds may be foraging at different locations or be influenced by temporal changes in the distribution and availability of prey. Many adult African Penguins from Robben and Dyer (34°41'S, 19°25'E) Islands abandon their nests in November and December each year, presumably to acquire reserves for their annual moult (Parsons & Underhill 2004, R.J.M. Crawford *in litt.*), further highlighting the critical timing of moult for survival.

In the inshore-foraging Yellow-eyed Penguin, *Megadyptes antipodes*, parents may continue to rear chicks, thereby delaying moult by weeks or even months, if feeding conditions deteriorate (van Heezik & Davis 1990). Humboldt Penguins at Punta San Juan, Peru, moult during the austral summer, when food supply is generally most abundant, suggesting that the timing of moult is critical to survival, and may constrain the time of breeding (Paredes *et al.* 2002). It seems likely that the constraints on the timing of moult are related to food availability, possibly a reflection of the substantial energy cost of the pre-moult fattening period (Gales *et al.* 1988). Energetically, moulting is more demanding than attending chicks (Croxall 1982, Adams & Brown 1990, Davis & Renner 2003). Although birds accumulating nutrients and energy reserves in the pre-moult fattening period are not constrained by the necessity to return to the colony to feed chicks, once they have initiated the moult process, they are unable to abandon the moult fast prematurely because their plumage would not be properly waterproofed. Consequently, penguins that have not accumulated sufficient energy reserves before moult will likely compromise their survival (Boersma 1976). In contrast, penguins which become energetically stressed while breeding, may abandon their breeding attempt in order to safeguard their own survival (Crawford & Dyer 1995). The acquisition of sufficient body reserves for moult is thus probably a greater priority than at any other time in the annual cycle.

The September–January moult peak of African Penguins at Dassen Island and most other South African colonies coincides with the spawning period for Sardine and Anchovy. For both these species, spawning generally takes place over the Agulhas Bank, from 30–130km offshore, mainly between September and February (Crawford & Shelton 1978, Hampton 1987, Armstrong & Thomas 1989). Breeding African Penguins in the Western Cape generally remain within 20km of their colonies when foraging; some breeding birds may forage up to 40km from their colonies (Heath & Randall 1989, Wilson *et al.* 1989, Wilson & Wilson 1995, Petersen *et al.* 2006). The spawning Sardine and Anchovy over the Agulhas Bank would therefore be beyond the foraging range of breeding African Penguins from Dassen Island, but would be accessible to nonbreeding penguins acquiring fat reserves for their moult. Changes in the relative abundance and distribution of Sardine and Anchovy are known to have significant impacts on the regional trends of penguin abundance (Crawford 1998, 1999, Crawford *et al.* 2001b). A Sardine-dominated system tends to favour penguin colonies between Lüderitz and Table

Bay, and an Anchovy dominated system would favour those colonies close to the Agulhas Bank, such as Dyer Island, due to the more consistently available food in these areas during the respective fish regimes (Crawford 1998). Although regime shifts in Sardine and Anchovy, as well as other environmental variables, will result in short and long-term changes in the abundance of prey resources available to penguins, the spawning patterns of these fish remain relatively stable and predictable. The strategy of penguins in South Africa to moult from September to January may therefore have evolved to coincide with a relatively predictable, but distant, source of food, and not necessarily be dictated by the breeding period alone.

Moult phenology of birds affected by the *Apollo Sea* and *Treasure* oil spills

Numbers of de-oiled *Apollo Sea* adults moulting at Dassen Island peaked in June and September 1995, earlier than the peak moult period for non-oiled flipper banded penguins in that year and the average seasonal peak for adult penguins at Dassen Island: November–December. Re-sighting effort was low up until December 1994, and so the moult pattern of *Apollo Sea* birds in the period after their release up until December 1994 was not well documented. It seems likely that the peaks in June and September 1995 were of de-oiled *Apollo Sea* birds moulting for the second time after their release, and that the first post-release moult would also have been earlier than the average seasonal pattern. At Robben Island the moult peak in 1994/95 was a month earlier than the normal peak, and was less synchronised (Underhill & Crawford 1999). This earlier moult was attributed to the *Apollo Sea* oil spill and the de-oiling and treatment process, which may have resulted in de-oiled *Apollo Sea* birds commencing moult earlier than usual (Underhill & Crawford 1999). About 74% of the birds that were oiled following the *Apollo Sea* spill were caught at Dassen Island (Dehrmann 1994). Similarly, 83% of the de-oiled birds re-sighted after release were seen at Dassen Island (Whittington 2002). The much larger number of de-oiled *Apollo Sea* birds at Dassen Island would suggest that the disruption of moult at Dassen Island in 1994/95 was at least as severe as at Robben Island. The larger number of de-oiled *Apollo Sea* birds from Dassen Island probably also explains the differences in the temporal extent of the disruption at the two colonies. At Robben Island, the moult returned to the normal seasonal peak the following year (1995/96), whereas at Dassen Island, the moult pattern of de-oiled *Apollo Sea* birds remained asynchronous with the rest of the colony in the 1995/96 season, becoming more synchronous thereafter.

The earlier moult of de-oiled birds following the *Apollo Sea* was probably due to the early termination of breeding activities; most de-oiled birds did not attempt to breed again in the first few months after their release, and were thus able to enter moult earlier than unaffected birds (Underhill & Crawford 1999). Other possible factors include mass-induced moult as a result of treated penguins gaining weight at the rehabilitation facilities (Kerley *et al.* 1985), disruption of hormonal cycles and the circannual clock (Otsuka *et al.* 2004), or physical damage to the plumage through oiling and/or cleaning forcing an early moult (Underhill & Crawford 1999).

The moult pattern of de-oiled birds following the *Treasure* spill conformed to the pattern for all adult-plumaged penguins at Dassen Island, both in the year following the spill and in relation to the average seasonal pattern, and suggests that there was less disruption to the moult cycles of de-oiled birds than was the case after the *Apollo Sea* spill. Following the *Treasure* spill, a total of 3 516 oiled birds were caught at Dassen Island and transported to the rehabilitation facilities (Chapter Six). This number is substantially less than the number of Dassen Island birds oiled after the *Apollo Sea* spill, and represents a small percentage of the total number of birds oiled following the *Treasure* spill. The majority of the approximately 19 000 that were oiled in the *Treasure* spill were caught at Robben Island (Crawford *et al.* 2000). However, when oiled, African Penguins generally make for the nearest breeding island or mainland beach (Underhill *et al.* 1999). Some of the oiled birds caught at Robben Island may therefore have been Dassen Island birds, but this is unlikely to change the magnitude of these proportions significantly.

The moult pattern of penguins at Robben Island following the *Treasure* spill was disrupted, as was the case after the *Apollo Sea* spill; the number of birds moulting peaked two weeks prior to the normal peak, primarily due to the earlier moult of the large number of de-oiled *Treasure* birds (Hemming 2001, Crawford *et al.* 2006a). The deviance from the normal moult peak was less than was found after the *Apollo Sea* spill at Robben Island (when the peak was one month earlier than the seasonal average); the pattern of moult in the year following the *Treasure* spill was also highly synchronised, in contrast to the reduced synchrony in moult after the *Apollo Sea* spill (Underhill & Crawford 1999, Hemming 2001). Hemming (2001) suggested that the smaller deviance

from the average moult peak and the greater synchronisation following the *Treasure* spill was due to the greater proportion of birds on Robben Island than in the *Apollo Sea* spill.

At Dassen Island the total number of adult-plumaged penguins moulting also peaked slightly earlier in 2000/01 than in previous years, but this was also the case in subsequent years. The probable explanation for the more synchronous moult pattern of de-oiled *Treasure* birds when compared with de-oiled birds from the *Apollo Sea* spill is that the former were kept in captivity for longer and released later in the year (i.e. closer to the average moult peak in November–December) from the rehabilitation centres. Both spills took place in June, but the much larger number of *Treasure* birds were kept at the rehabilitation centres for 30% longer than birds contaminated after the *Apollo Sea* spill (Barham *et al.* 2007). As was the case with the *Apollo Sea* birds, most de-oiled birds from the *Treasure* spill appear not to have initiated further breeding attempts upon their return to Dassen Island, but rather commenced with preparations for their annual moult. The later release of the *Treasure* birds would have resulted in them moulting closer to the average moult peak than the de-oiled *Apollo Sea* birds.

The asynchronous and later moult of *Treasure* evacuees in 2000/01 was almost certainly due to these birds attempting to breed again soon after their return from Cape Recife in the Eastern Cape, thereby delaying moult beyond the normal peak, and also accounting for the broader peak of moult. The high level of breeding and the short lag between the return of the evacuees and their first breeding attempts were likely influenced by the greatly enhanced availability of food at the time (van der Lingen *et al.* 2001, Barange *et al.* 2004, Crawford *et al.* 2006b). Coincident with the increased food availability, was the rapid increase in most African Penguin colonies in the Western Cape (Wolfaardt *et al.* 2001). The rapid response of the evacuated birds to these conditions and the lack of immediate response by the de-oiled birds highlights further the inability of most de-oiled birds to breed soon after their release from the rehabilitation centres.

If timing of moult is critical to survival of African Penguins, then one would expect any disruptions to the regular pattern to manifest in energetic costs and possibly increased mortality rates. Whether the disruption to the moult cycles of de-oiled *Apollo Sea* birds and the *Treasure* evacuees has negatively influenced the survival of these birds is not

known with certainty, but seems unlikely. The survival of de-oiled penguins from the *Apollo Sea* spill has been shown to be indistinguishable from birds that were not oiled (Whittington 2002). The favourable feeding conditions during much of this study probably helped offset potentially negative impacts of disrupted moult cycles.

Intervals between moults

The mean interval between successive moults for African Penguins at Dassen Island of 349 days was slightly less than mean of 368 days (SD = 24.5, *n* = 152) reported by Randall & Randall (1981) for penguins at St. Croix Island and 367 days (SD = 49.2, *n* = 137) reported by Kemper (2006) for Namibian penguins, but less than the 321 days (SD = 30, *n* = 11) calculated by Cooper (1978) for penguins at Dassen Island in the early 1970s. Cooper (1978) suggested that the moult interval for African Penguins was sub-annual, reflecting the sub-annual breeding pattern of birds (Cooper 1980). In Cooper's (1980) study the mean interval between successful breeding attempts was 10.5 months, the same as the mean interval between successive moults (Cooper 1978). Moult intervals varied widely for individuals in this study, from 221 days to 546 days, and so Cooper's (1978) estimates, based on a small sample size, may not be representative. Furthermore, the incidence of replacement and second clutches in my study appears to be far greater than reported by Cooper (1980), which may have extended the duration of the inter-moult periods. The shortest and longest moult intervals reported here for adult African Penguins are lower and higher than previous estimates (Cooper 1978, Randall & Randall 1981, Kemper 2006), respectively, probably as a result of the substantially larger sample size (*n* = 701 records) than in earlier studies.

The wide range of consecutive moult intervals indicates that although the duration of the inter-moult period for African Penguins is about one year, individuals have some degree of flexibility in the timing of their moult. This flexibility is probably due to the protracted nature of the breeding season. Moult intervals were longest in the periods 1998–1999 and 2000–2001. During these periods, breeding success was high and the availability of food was greatly increased (Chapter Five). These conditions would likely contribute towards an increased frequency of replacement and second clutches, thus extending the interval between successive moults. Indeed, the median time elapsed between the completion of a successful breeding attempt and the initiation of a second clutch was highest for birds in Breeding Study 16, which took place in the first half of 1999 (Chapter

Five). Re-sightings of flipper-banded birds (where these were sufficient to establish the reason for a longer inter-moult interval) further support the view that long moult intervals were related to prolonged breeding activities. The longer inter-moult intervals for the period 2000–2001 may also have been influenced by the moult patterns of the *Treasure* evacuees reverting to the "island pattern" of moult after the initial disruption.

The shortest average inter-moult intervals were measured in 2002–2003 and 2003–2004. Breeding success data for birds at Dassen Island during this period are not available; however, breeding success of African Penguins at nearby Robben Island over the period 2001–2005 was lowest in 2003 and 2004 (Barham *et al.* 2007). Although feeding conditions at the time of breeding are likely to influence the degree to which birds re-lay clutches, the effect on moult intervals is not necessarily straightforward. For example, during unfavourable conditions when breeding success is likely to be lower, many birds lay replacement clutches after failed breeding attempts (Chapter Five), thus also potentially extending the inter-moult period. In addition, breeding success in many long-lived seabirds is also influenced by factors other than environmental constraints, such as the variation in intrinsic adult quality, age and experience (Ainley *et al.* 1983, Pugasek & Diem 1983, Dann & Cullen 1990, Daunt *et al.* 2001), which in turn may influence the likelihood of re-laying clutches and the duration of the inter-moult period.

Intervals between breeding and moult

For penguins which are able to breed throughout the year, the question of whether the birds moult pre- or post-nuptially is largely redundant. Indeed, African Penguins have the flexibility of being able to moult either before or after they breed. The annual cycle of African Penguins needs to incorporate and balance both breeding activities and moult. Although the mean intervals between breeding and moult and moult and breeding are similar, there is again considerable individual variation in both. These intervals relate, at least partly, to the time required to acquire sufficient energy reserves for moult and to recover lost condition (and attain sufficient reserves to initiate breeding) after moult and before breeding, respectively. Other factors, such as the time required to reunite with previous mates or establish new mates, and the courtship period also influence the interval between moult and breeding.

Penguins have the capacity to accumulate energy reserves for moult quickly when food is available (Adams & Brown 1990), and would benefit from favourable feeding conditions close to the breeding colony, by reducing the period required to attain the necessary body condition for moult. Similarly, the shorter interval between moult and breeding in some years of this study probably relates to improved feeding conditions at these times, and the ability of birds to recover lost physiological condition rapidly following moult. The years in which the longest intervals between moult and breeding were recorded, 1995 and 2004, correspond to years of relatively low breeding success and reduced food availability (and lower breeding success at Robben Island), respectively. The shortest intervals between moult and breeding were recorded in 1999 and 2003. The former period was one in which feeding conditions were favourable and breeding success was high. However, 2003 was considered to be less favourable based on the low breeding success of birds at Robben Island (Barham *et al.* 2007). The short intervals between moult and breeding during this period are thus more difficult to explain, but may have been influenced by favourable local foraging conditions that did not persist throughout the year.

Fidelity of moulters to colonies

The majority of African Penguins at Dassen Island moulted in the same monitoring area year after year. They also moulted in the same area in which they bred. Close to 70% of flipper-banded birds recorded moulting, did so along the coast adjacent to the breeding colony in which they bred. The remaining 30% moulted at nest sites, again predominantly in the same colony in which they bred. In many instances, birds moulted in their own nest sites, and occasionally moulted together with their mate. The strategy of returning to the same area and colony to moult is presumably associated with the high fidelity to nest sites (Randall 1983), and the maintenance of pair bonds and pair synchrony. This, in turn, may facilitate better co-ordination of breeding activities between pairs and enable pairs to initiate breeding attempts quickly in response to improved feeding conditions.

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Table 3.1 Inter-nest distances (cm) of African Penguin burrow nests in burrow occupancy survey areas, Dassen Island.

Area	Mean	SD	Max	Min	*n*
A	89.57	38.1	180	13	30
B	133.5	89.2	372	38	30
D	94.17	45.44	223	34	30
F	95.73	56.6	260	33	30
G	127.23	70.81	400	26	30

Table 3.2 Mean and median percentages of African Penguin burrows at Dassen Island that were unoccupied in burrow occupancy surveys for the period December 1994-September 2006 for Areas B, D, F and G, and May 1997 - September 2006 for Area A. The actual counts and percentages were used to calculate the mean and standard deviation, and not the interpolated figures (see text for further details).

Area	Mean	SD	Median	*n*
A	49.50	18.04	45.78	167
B	42.70	14.41	41.73	223
D	46.68	13.45	45.93	220
F	39.30	12.98	37.86	212
G	36.67	12.72	36.24	237

Table 3.3 Spearman rank correlation coefficients of the number of African Penguins from each study group incubating eggs with the proportion of burrows containing incubating adults from the relevant colony at Dassen Island.

Study Group	Correlation coefficient (r_s)	*n*	*P*	Time period
De-oiled *Apollo Sea* birds, Area B	0.4442	120	*P*<0.001	January 1995 - December 2004
De-oiled *Apollo Sea* birds, Area G	0.5407	120	*P*<0.001	January 1995 - December 2004
De-oiled *Treasure* birds, Area B	0.5002	54	*P*<0.001	July 2000 - December 2004
De-oiled *Treasure* birds, Area F	0.6527	54	*P*<0.001	July 2000 - December 2004
De-oiled *Treasure* birds, Area G	0.5501	54	*P*<0.001	July 2000 - December 2004
Evacuated *Treasure* birds, Area B	0.6737	54	*P*<0.001	July 2000 - December 2004
Evacuated *Treasure* birds, Area F	0.6609	54	*P*<0.001	July 2000 - December 2004
Evacuated *Treasure* birds, Area G	0.7137	54	*P*<0.001	July 2000 - December 2004

Table 3.4 Moult intervals (days) per year for African Penguins at Dassen Island.

Year	Mean	SD	Median	Min	Max	*n*
1994-95	344.00	39.60	344	316	372	2
1995-96	347.01	45.54	343	223	545	131
1996-97	343.89	35.89	344	257	457	148
1997-98	352.52	47.18	355	201	513	97
1998-99	360.68	51.74	355	277	546	103
1999-2000	349.90	41.92	347	228	515	73
2000-01	360.19	36.17	361	263	434	57
2001-02	343.59	38.76	349	238	446	49
2002-03	326.84	51.15	337	237	408	25
2003-04	326.29	36.72	334	252	387	14
2004-05	341.00	98.99	341	271	411	2
All years	349.08	44.02	348	201	546	701

Table 3.5 Flipper-banded African Penguins at Dassen Island with moult intervals less than 280 days.

RingNo	Moult 1	Moult 2	Interval (days)	Period
A01019	10/11/1997	06/08/1998	269	97-98
A01867	29/11/1999	14/08/2000	259	99-00
A02470	14/11/2001	14/08/2002	273	01-02
A05949	27/06/2002	24/03/2003	270	02-03
A14347	04/10/2001	22/06/2002	261	01-02
A14503	08/05/2002	17/01/2003	254	02-03
A14540	24/08/2002	18/04/2003	237	02-03
A14649	17/03/2004	13/12/2004	271	04-05
A14659	22/06/2002	19/02/2003	242	02-03
A14742	08/04/2002	07/01/2003	274	02-03
A15190	16/03/2001	04/12/2001	263	00-01
L03958	25/02/2003	29/11/2003	277	03-04
L08549	13/09/2002	23/05/2003	252	02-03
M00925	21/07/2001	16/03/2002	238	01-02
S03363	09/09/1996	04/06/1997	268	96-97
S10116	11/06/1997	05/03/1998	267	97-98
S11777	14/02/1996	17/11/1996	277	96-97
S19425	23/01/2003	02/10/2003	252	03-04
S20996	02/02/1997	01/11/1997	272	97-98
S21094	05/09/1995	24/05/1996	262	95-96
S21283	20/06/1995	20/03/1996	274	95-96
S21363	24/06/1999	07/02/2000	228	99-00
S21768	11/12/1995	13/09/1996	277	95-96
S21794	24/12/1998	27/09/1999	277	98-99
S21886	27/04/1997	21/01/1998	269	97-98
S22507	18/09/1997	17/05/1998	241	97-98
S22716	24/05/1999	01/02/2000	253	99-00
S22738	28/08/1997	20/05/1998	265	97-98
S23102	29/07/1996	04/05/1997	279	96-97
S23586	26/09/1995	18/06/1996	266	95-96
S24891	31/10/1995	10/06/1996	223	95-96
T02987	13/08/1996	27/04/1997	257	96-97

Table 3.6 Interval between successive moults for African Penguins that were recorded moulting in more than two successive years at Dassen Island.

No. successive years	*n*	Interval (days)			
		Mean	SD	Min	Max
3	36	350.25	44.63	252	546
4	16	351.59	37.87	270	521
5	4	361.00	40.39	253	424
6	1	365.17	36.11	317	421

Table 3.7 Interval in days between the completion of breeding and the mid-point of moult for African Penguins monitored in study nests at Dassen Island. The year refers to the calendar year in which the bird moulted.

Year	Mean	SD	Median	Min	Max	*n*
1995	113.74	66.70	105	23	279	34
1996	92.33	56.45	85	9	293	55
1997	107.62	57.26	110	11	241	37
1998	80.35	45.28	69	8	193	43
1999	88.94	49.71	76	7	218	50
2000	113.97	73.46	102	20	342	35
All years	97.71	58.56	86	7	342	254

Table 3.8 Interval in days between the mid-point of moult and estimated date of egg-laying for African Penguins at Dassen Island. The year refers to the calendar year in which the bird moulted.

Year	Mean	SD	Median	Min	Max	*n*
1995	125.16	70.78	105	32	359	161
1996	97.46	51.43	86	29	329	327
1997	119.78	76.99	92	29	29	137
1998	102.21	64.35	77.5	33	351	188
1999	88.82	56.49	69	31	322	209
2000	96.41	55.54	76	29	337	195
2001	105.73	64.81	86	29	358	172
2002	103.75	57.73	89	26	351	103
2003	85.94	45.45	68	29	239	69
2004	120.48	52.90	116	31	257	29
All years	102.79	61.37	83	29	360	1590

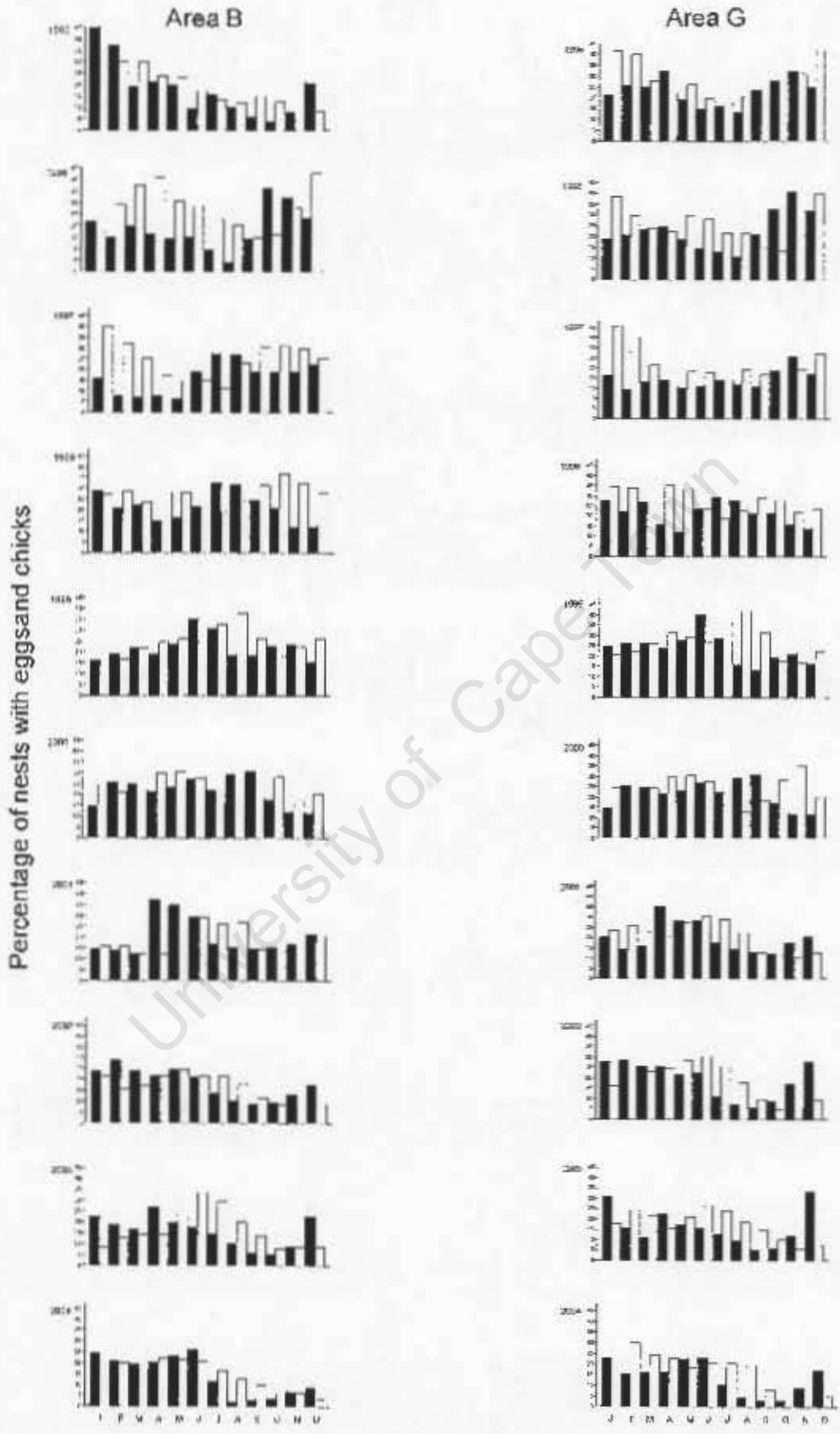

Figure 3.1 Proportion of African Penguin burrows at Dassen Island containing eggs (black bars) and chicks (white bars) per year for Areas G and B.

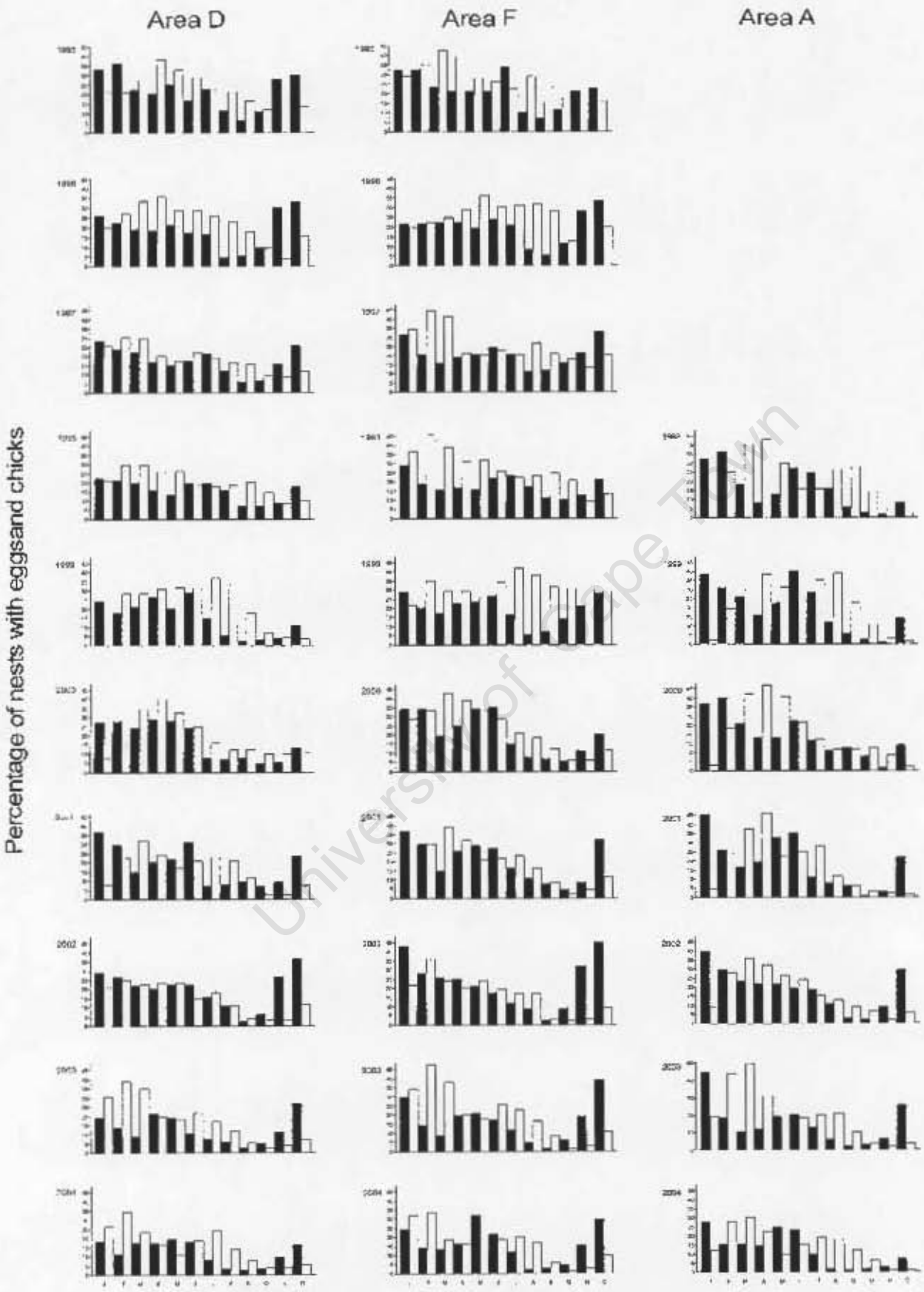

Figure 3.1 (cont.) Proportion of African Penguin burrows at Dassen Island containing eggs (black bars) and chicks (white bars) per year for Areas D, F and A.

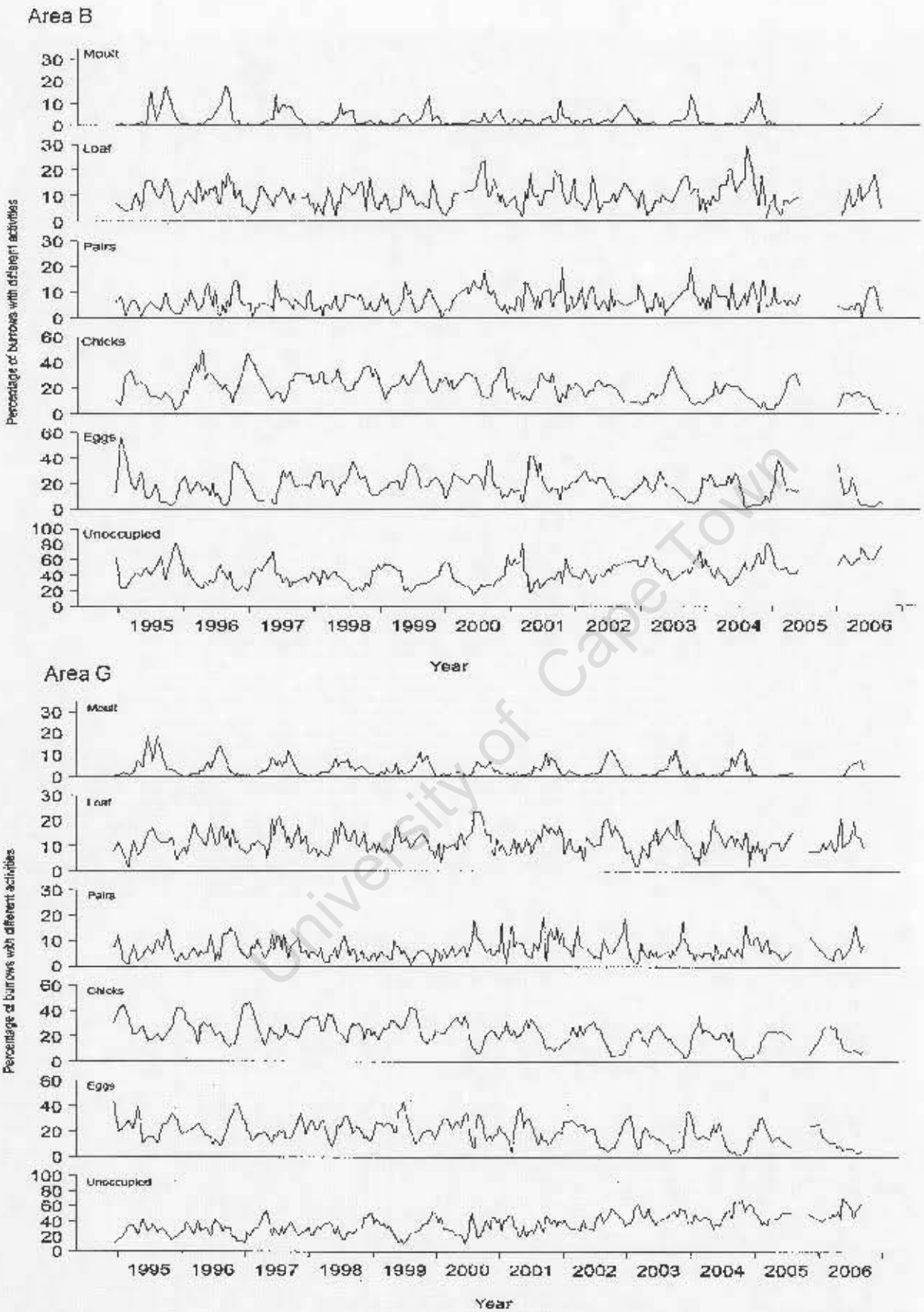

Figure 3.2 African Penguin burrows in Areas B and G at Dassen Island with different activities. The lines represent the interpolated percentages of burrow nests with Egg(s), Chick(s), Pair(s), Loafer(s), Moulter(s) and the percentages that were unoccupied (see text for further details) per day from 1995 to September 2006. Activity categories were mutually exclusive, and the composite figures per day sum to 100%. Gaps in the lines indicate no data.

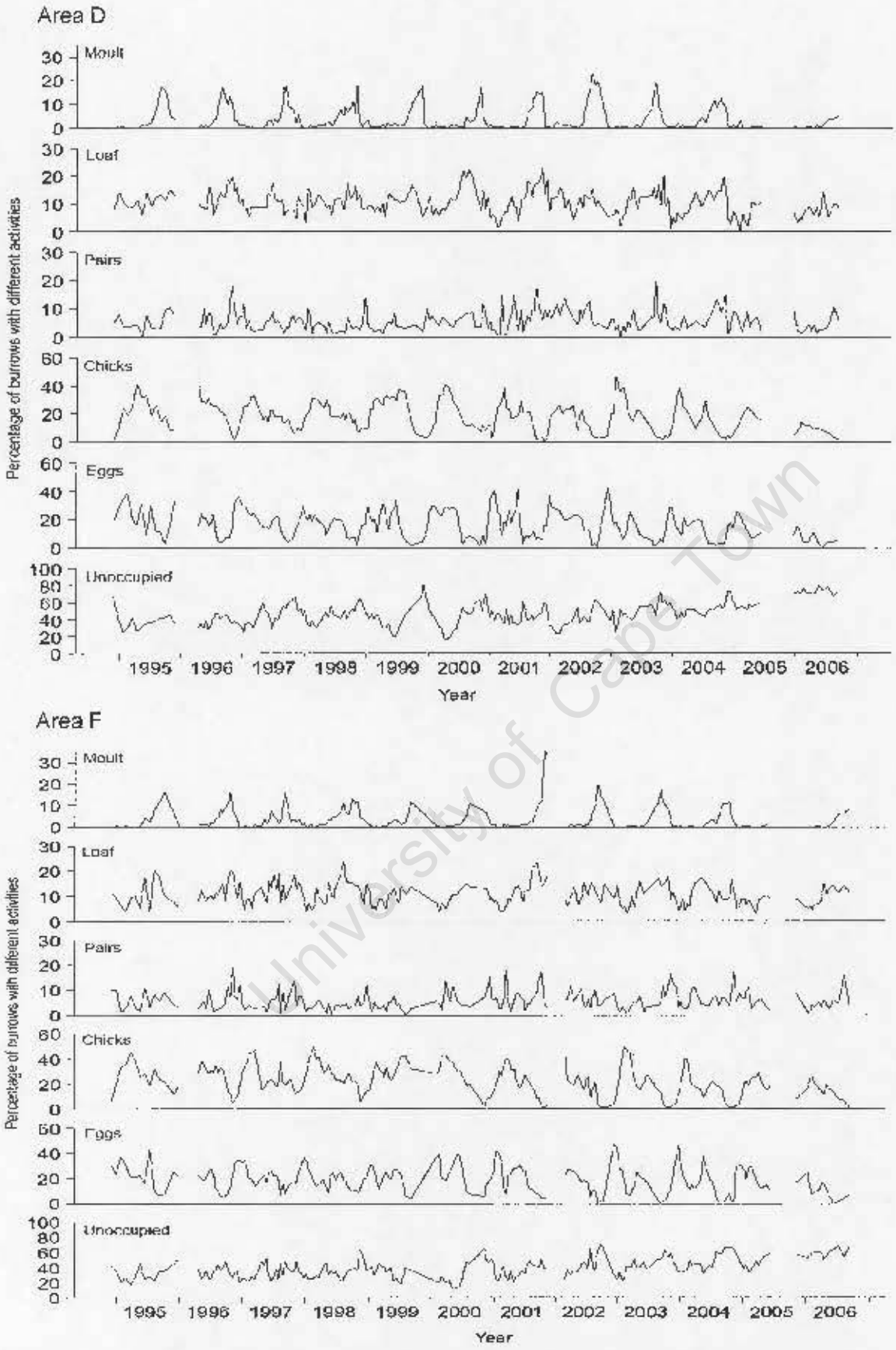

Figure 3.2 (cont.) African Penguin burrows in Areas D and F at Dassen Island with different activities. The lines represent the interpolated percentages of burrow nests with Egg(s), Chick(s), Pair(s), Loafer(s), Moulter(s) and the percentages that were unoccupied (see text for further details) per day from 1995 to September 2006. Activity categories were mutually exclusive, and the composite figures per day sum to 100%. Gaps in the lines indicate no data.

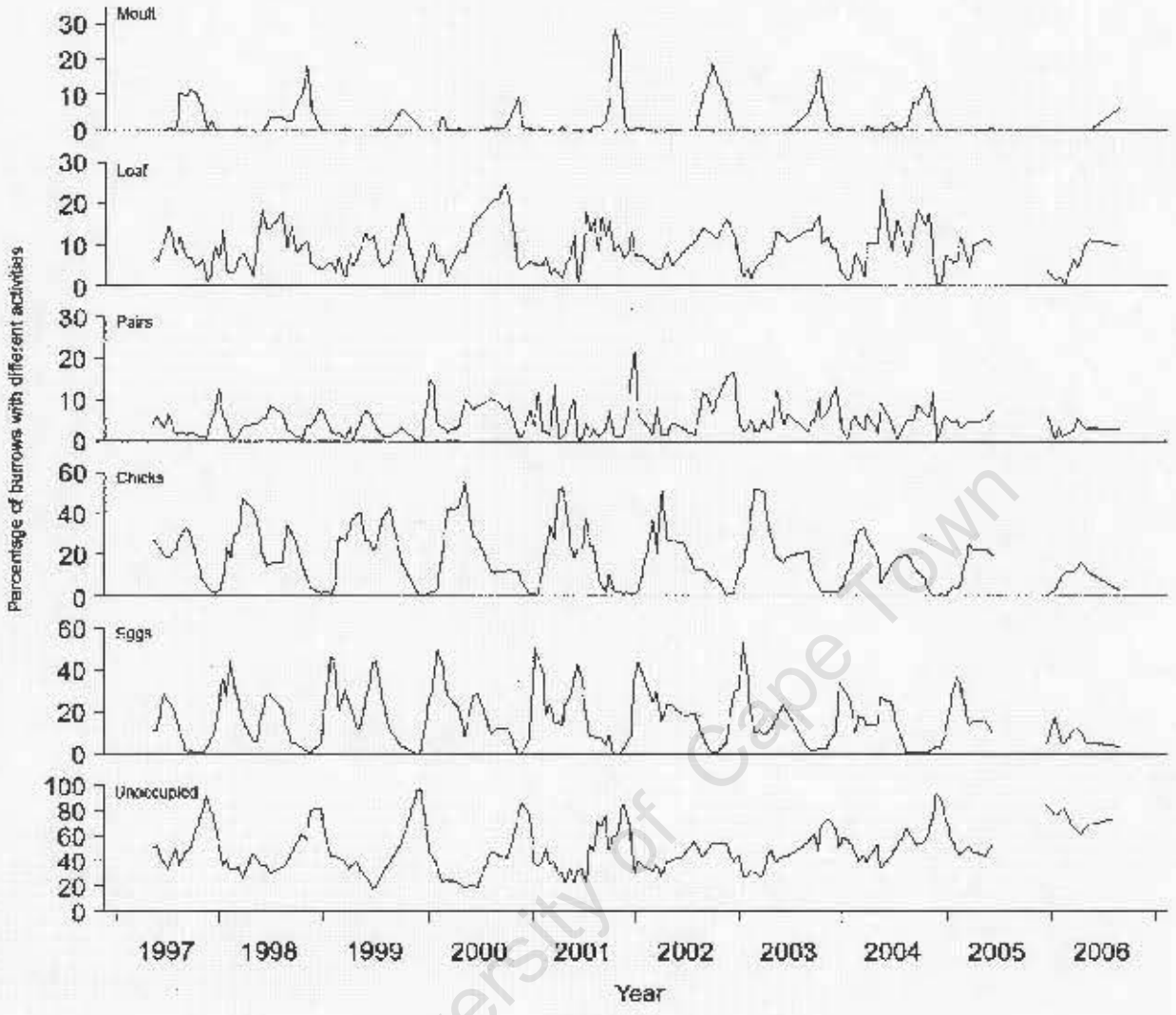

Figure 3.2 (cont.) African Penguin burrows in Area A at Dassen Island with different activities. The lines represent the interpolated percentages of burrow nests with Egg(s), Chick(s), Pair(s), Loafer(s), Moulter(s) and the percentages that were unoccupied (see text for further details) per day from 1995 to September 2006. Activity categories were mutually exclusive, and the composite figures per day sum to 100%. Gaps in the lines indicate no data.

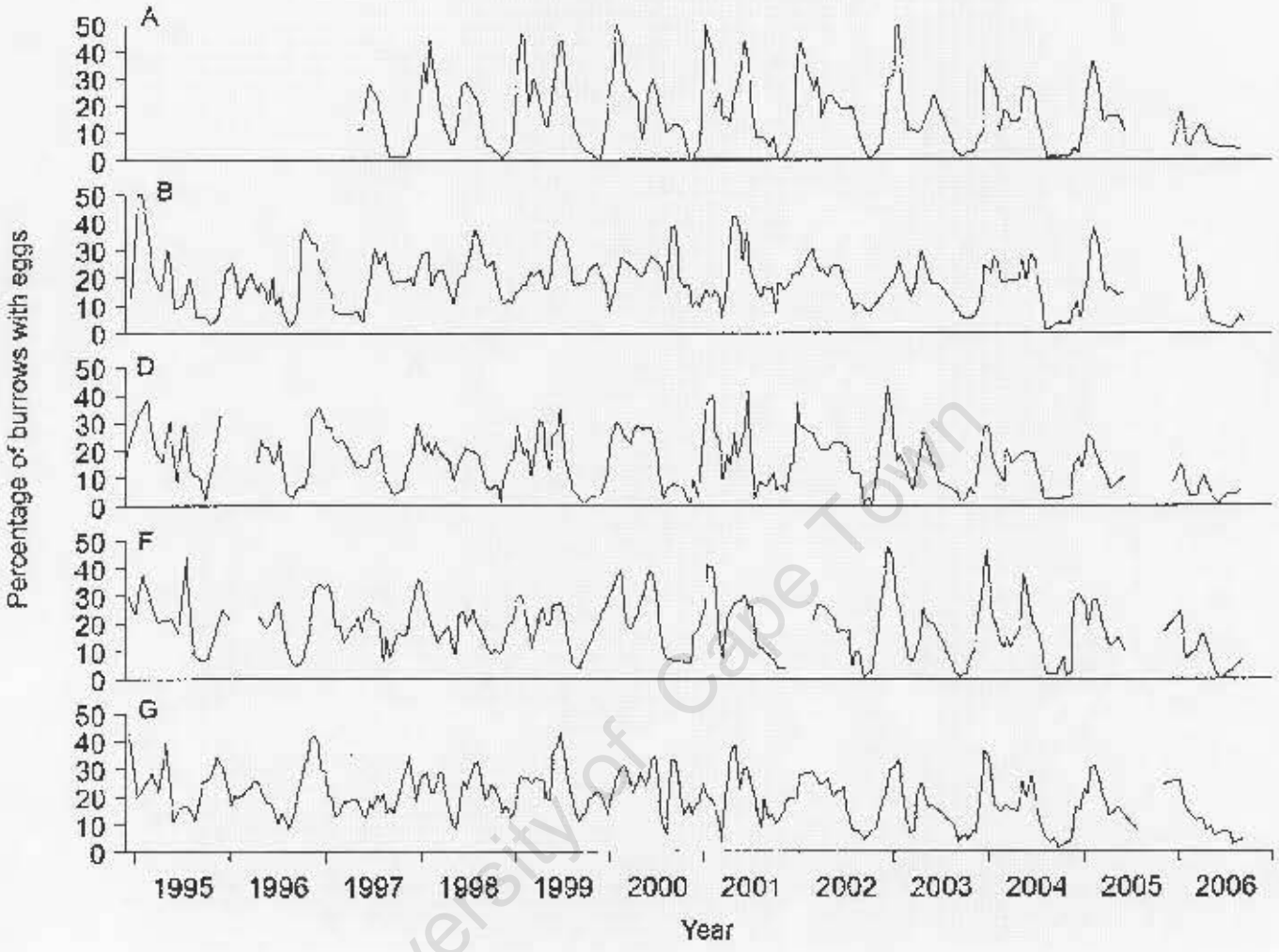

Figure 3.3 Percentage of burrows with African Penguins incubating eggs in study areas A, B, D, F and G at Dassen Island. The lines represent daily interpolated percentages. Gaps in the lines indicate no data.

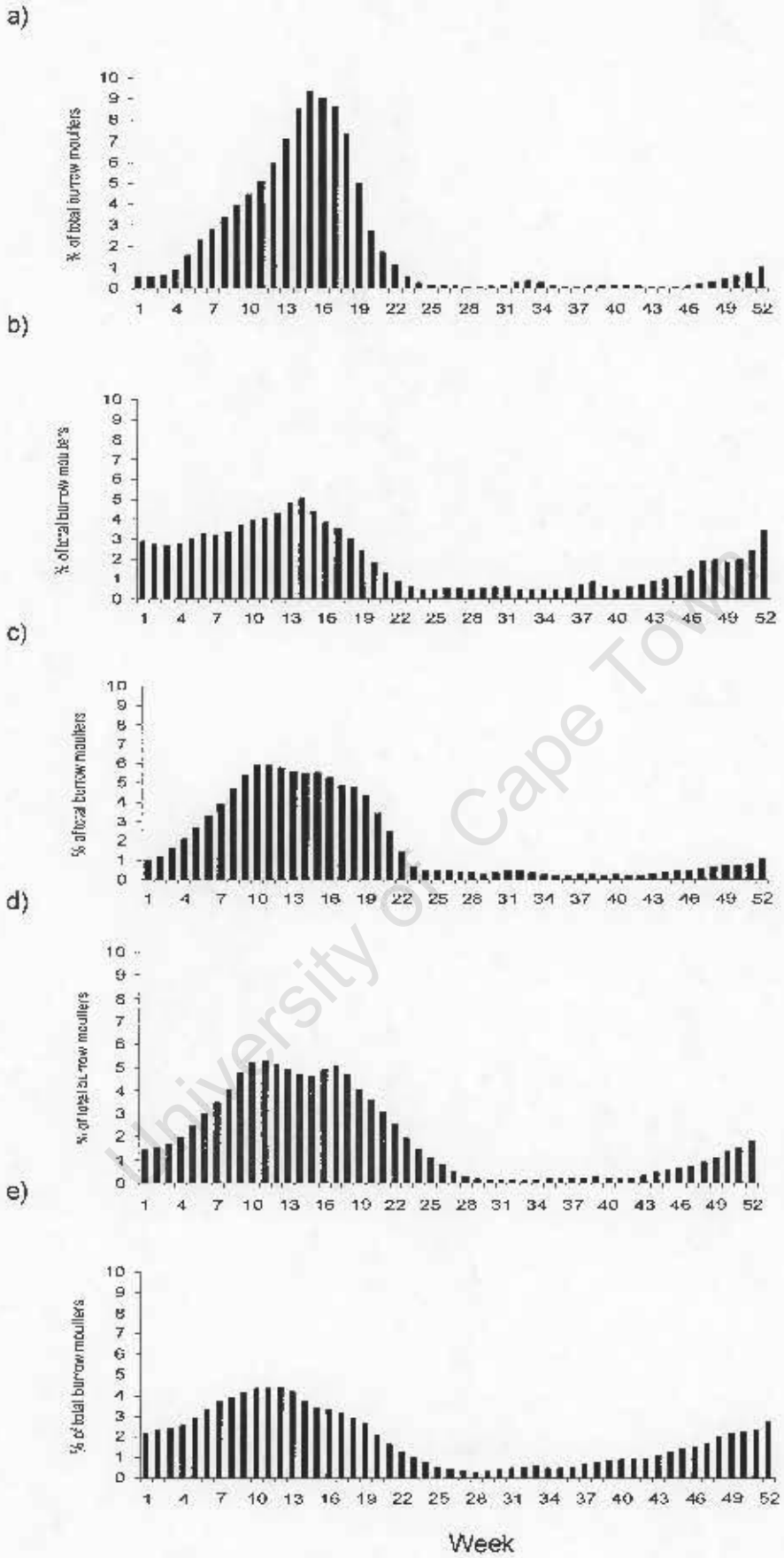

Figure 3.4 Seasonal pattern of moulting in burrows for African Penguins at Dassen Island. The pattern indicates the percentage of the total number of burrows with moulters in each week. Week 1 starts 1 July, Week 52 ends 29 June for a) Area A, b) Area B, c) Area D, d) Area F and e) Area G.

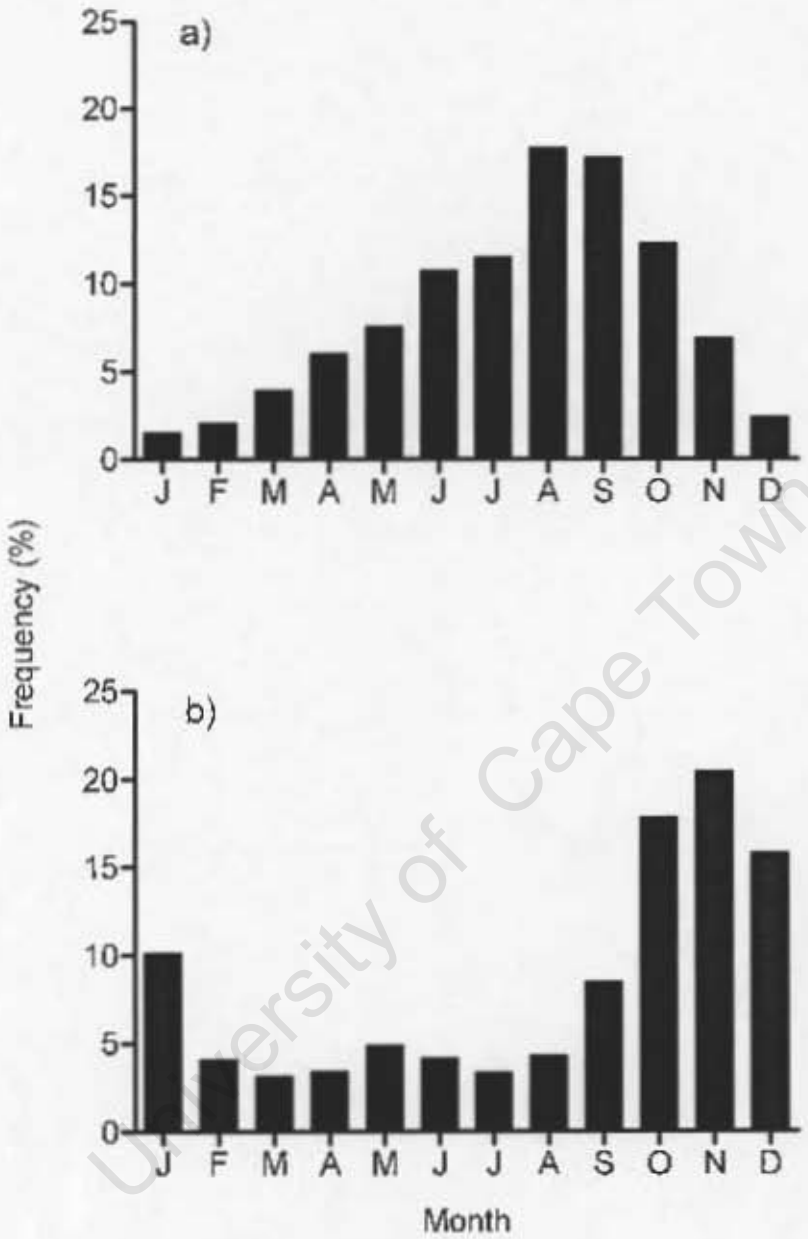

Figure 3.5 Frequency of re-sightings of flipper-banded African Penguins moulting a) in nests, and b) on the coast at Dassen Island.

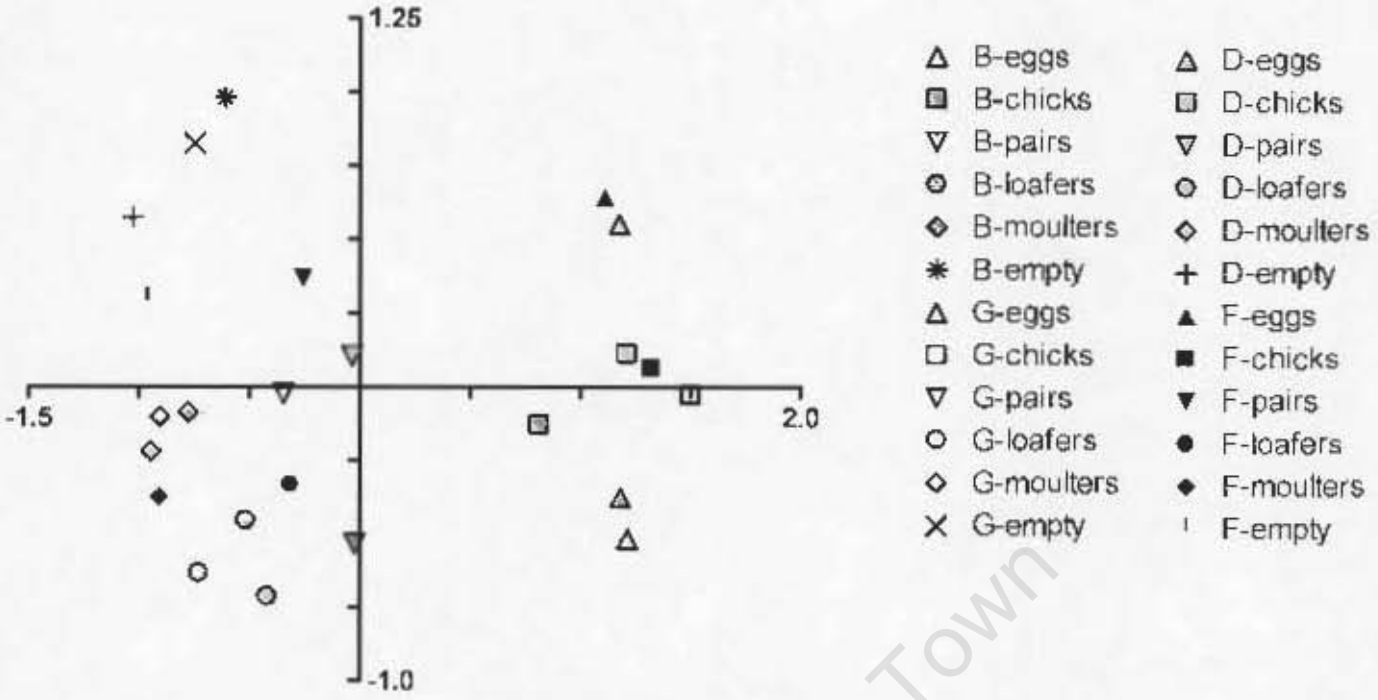

Figure 3.6 Plots of the percentage of burrows with different activities for four study areas (B, D, F and G) and all years (1995-2004) using non-metric multidimensional scaling (see text). Area A was excluded because of the shorter monitoring period. 2005 was excluded due to incomplete data.

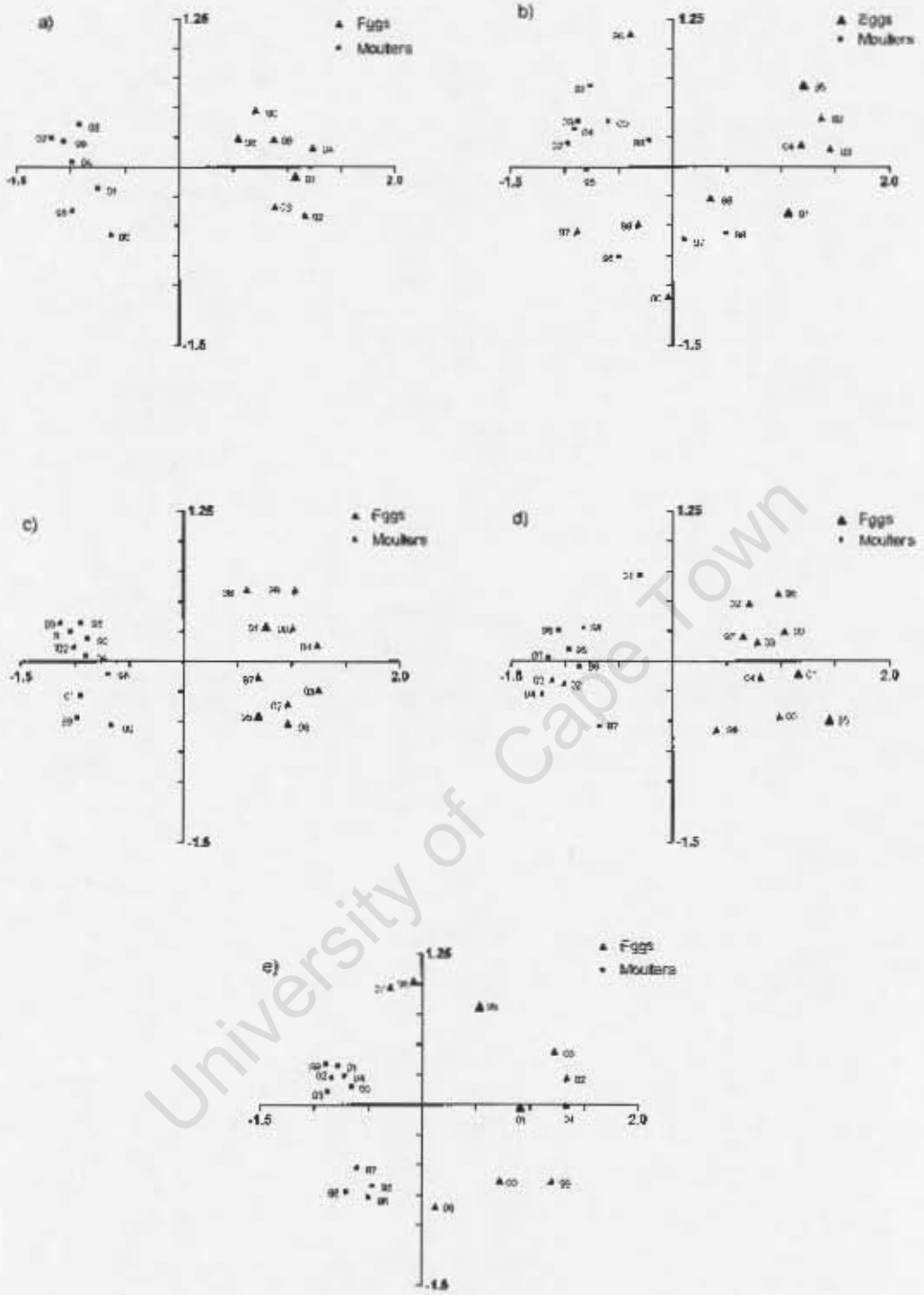

Figure 3.7 Plots produced from non-metric multidimensional scaling of the proportion of burrows containing adult African Penguins incubating eggs and moulting at Dassen Island for a) Area A, b) Area B, c) Area D, d) Area F and e) Area G.

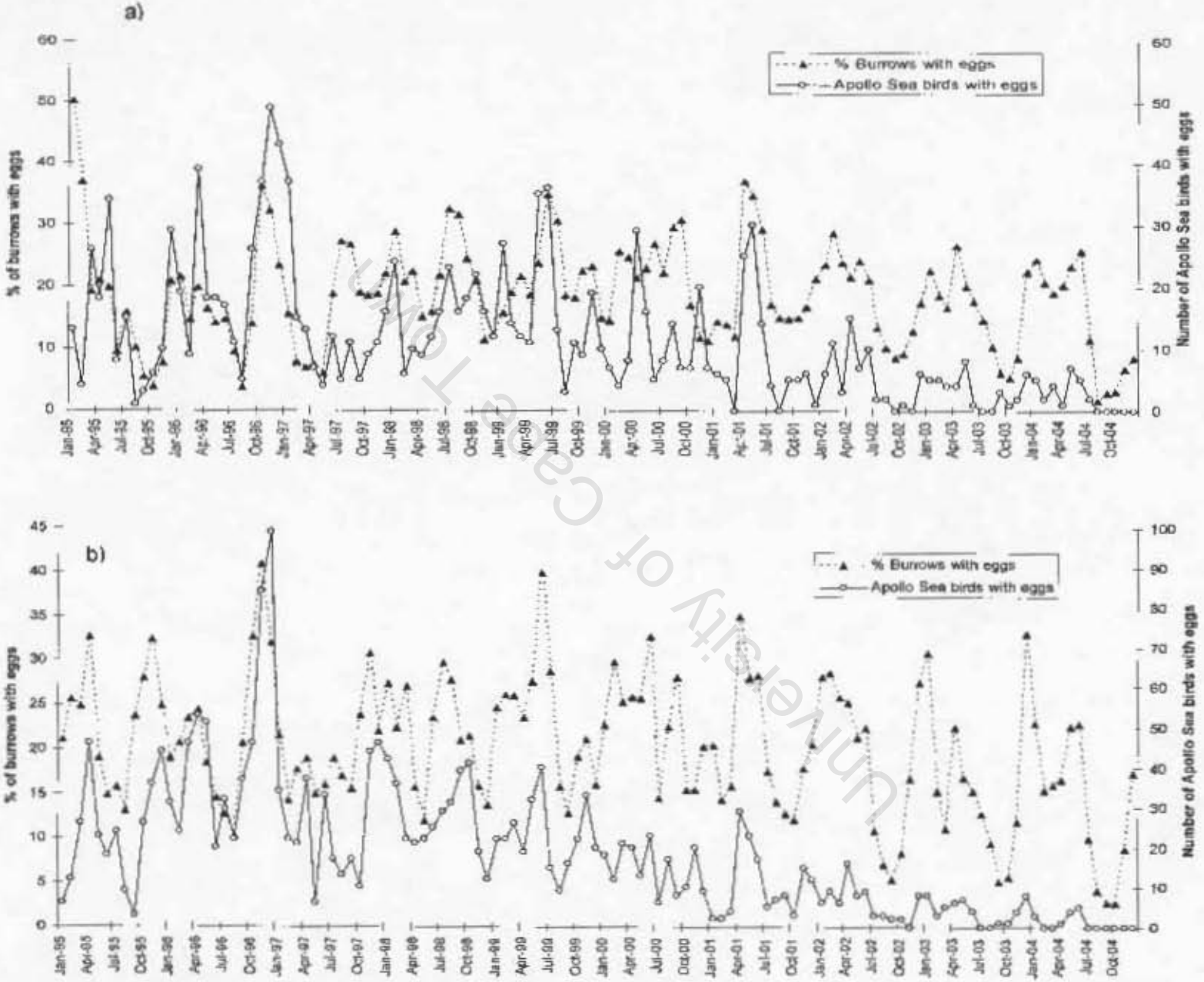

Figure 3.8 The number of de-oiled *Apollo Sea* African Penguins incubating eggs and the total proportion of burrows containing incubating adults in a) Area B and b) Area G at Dassen Island for the period January 1995–December 2004.

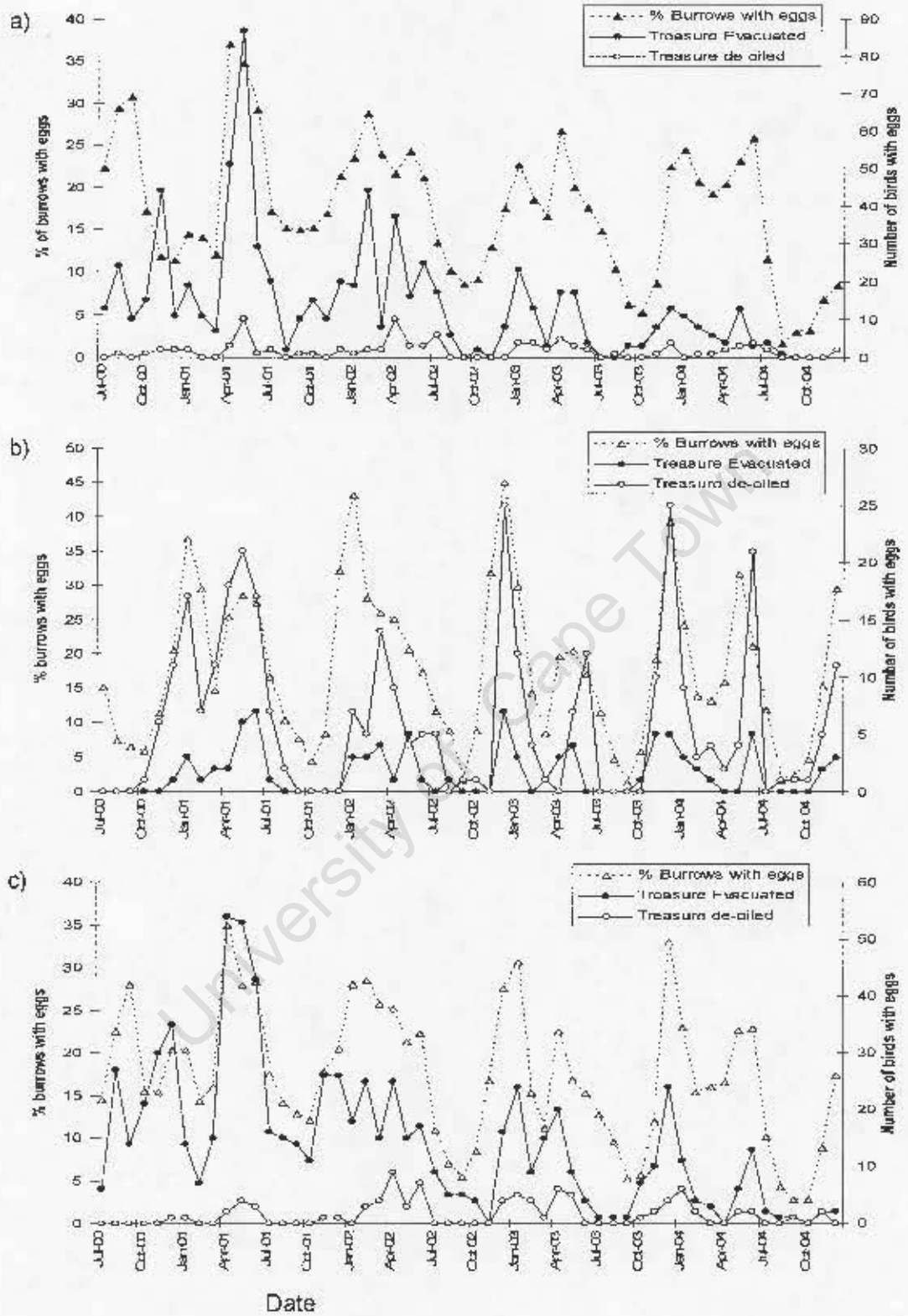

Figure 3.9 The number of de-oiled and evacuated *Treasure* African Penguins incubating eggs and the total proportion of burrows containing incubating adults in a) Area B and b) Area F and c) Area G at Dassen Island for the period July 2000–December 2004.

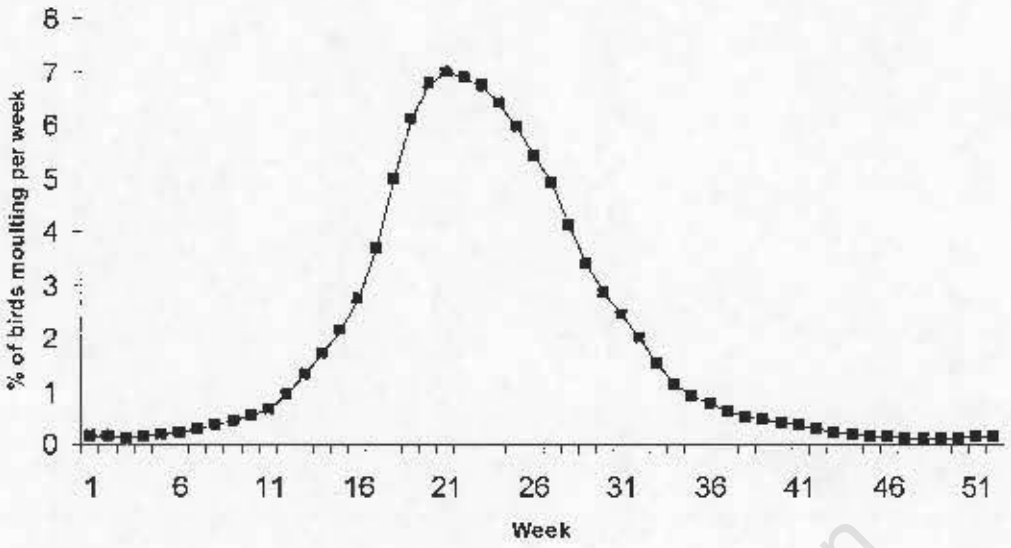

Figure 3.10 Percentage of African Penguins in adult plumage moulting along the coast each week at Dassen Island.

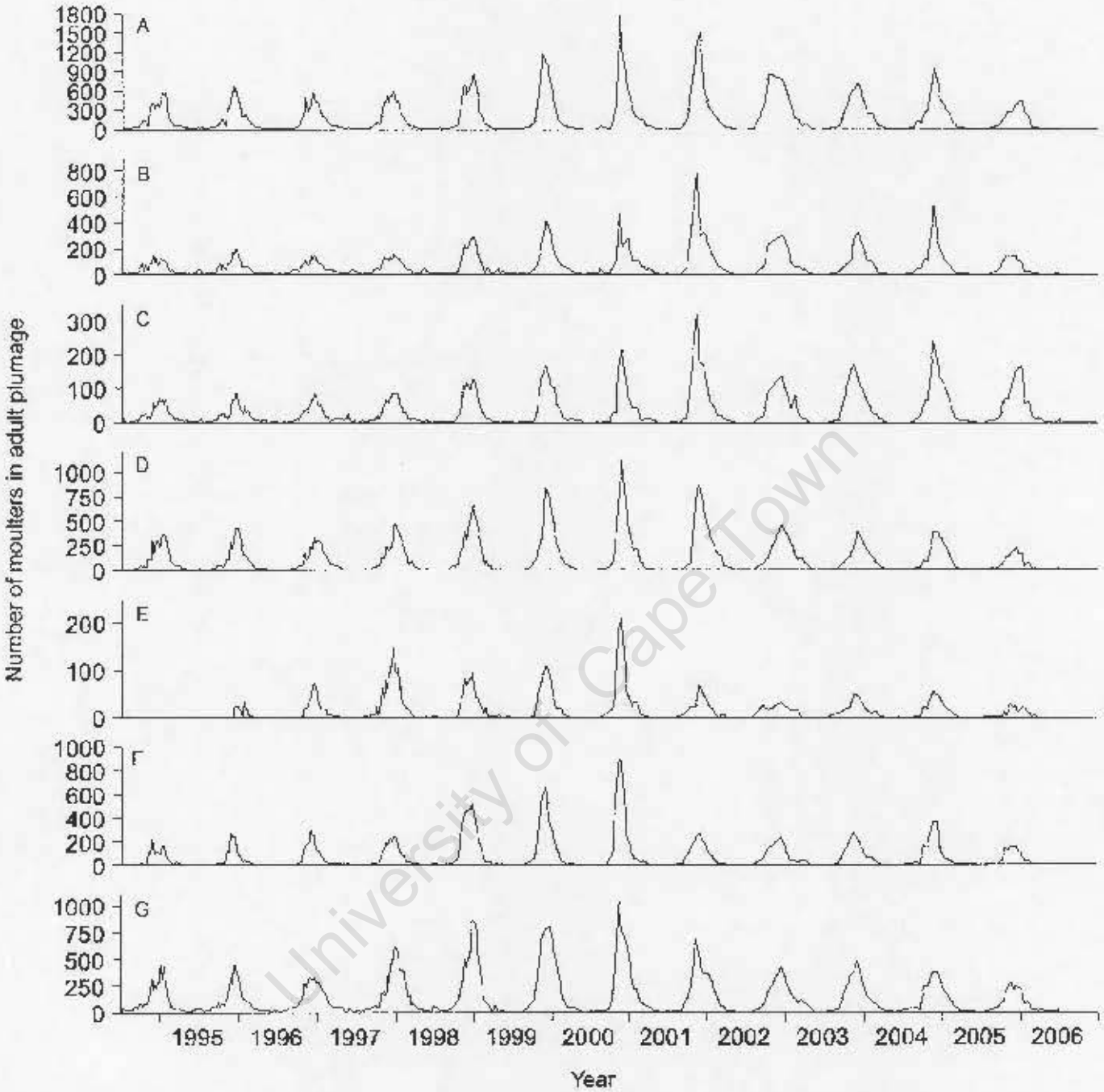

Figure 3.11 Interpolated counts of African Penguins moulting in each coastal monitoring area at Dassen Island, November 1994–September 2006.

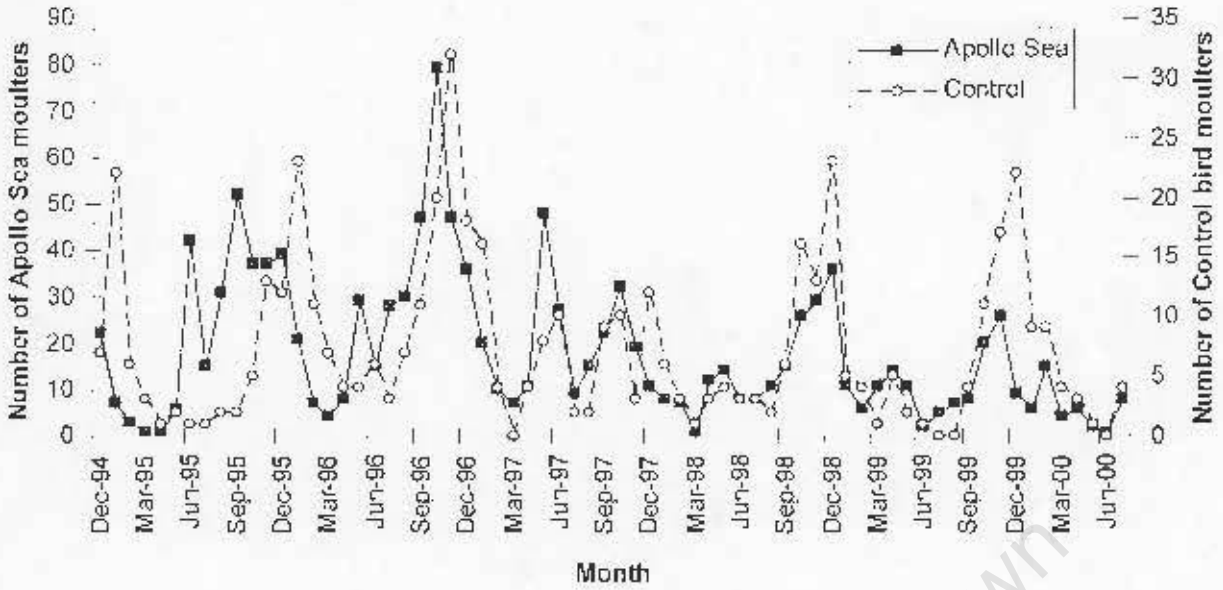

Figure 3.12 Numbers of de-oiled African Penguins involved in the *Apollo Sea* spill and un-oiled flipper-banded (control) birds moulting per month at Dassen Island.

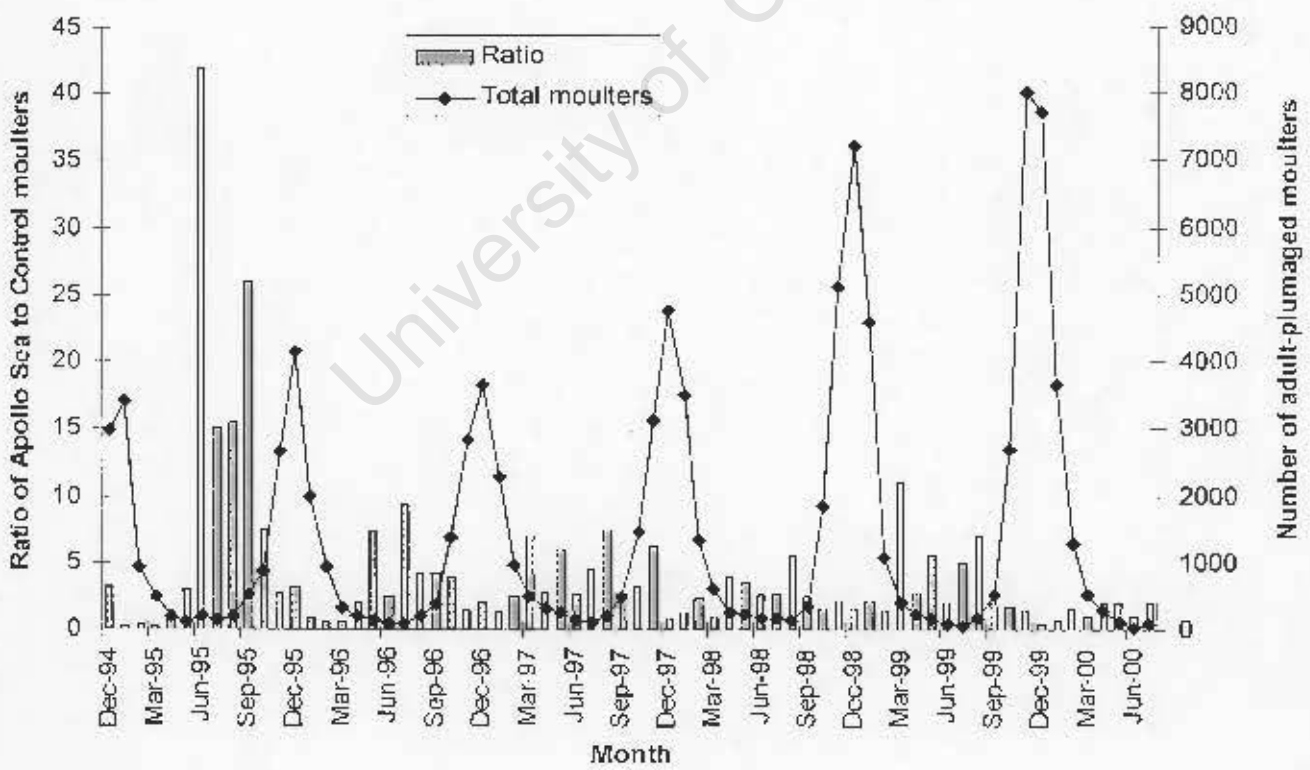

Figure 3.13 Total numbers of African Penguins moulting along the coast and the ratio of *Apollo Sea* moulters to un-oiled flipper-banded (control) moulters per month at Dassen Island.

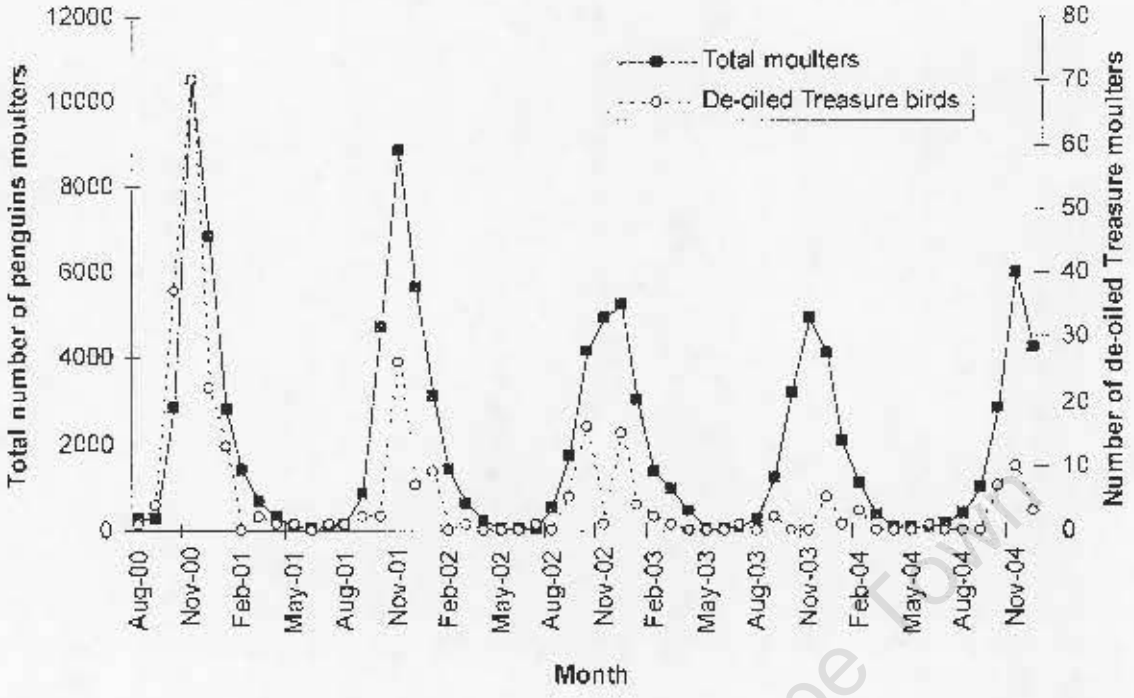

Figure 3.14 Total numbers of African Penguins in adult-plumage and de-oiled *Treasure* adults moulting along the coast at Dassen Island, August 2000–December 2004

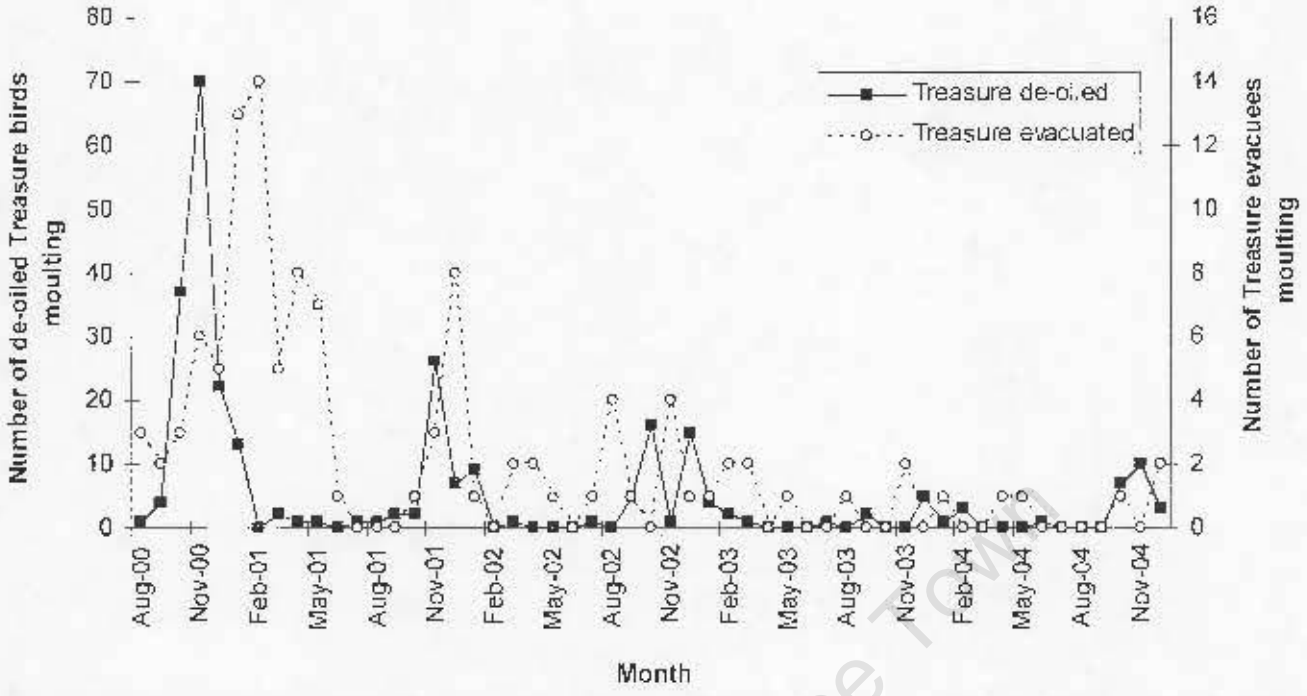

Figure 3.15 Numbers of de-oiled and evacuated African Penguins involved in the Treasure oil spill moulting along the coast at Dassen Island, August 2000–December 2004.

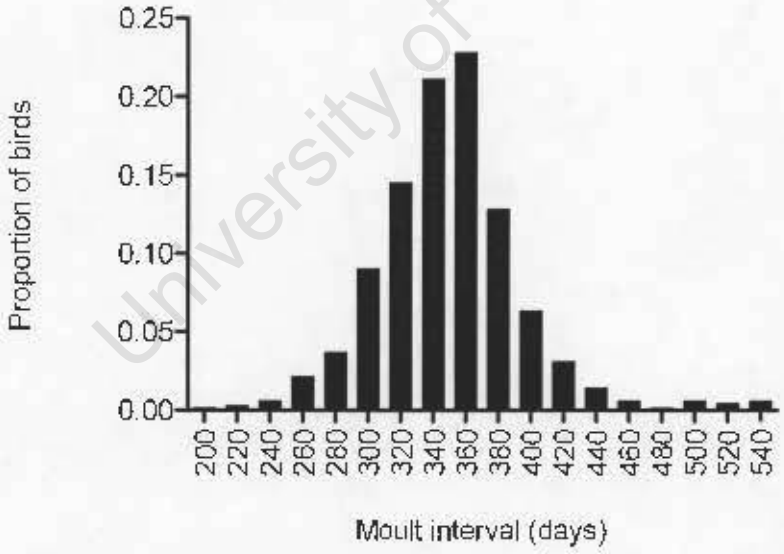

Figure 3.16 Frequency distribution of intervals between successive moults for flipper-banded African Penguins in adult plumage at Dassen Island.

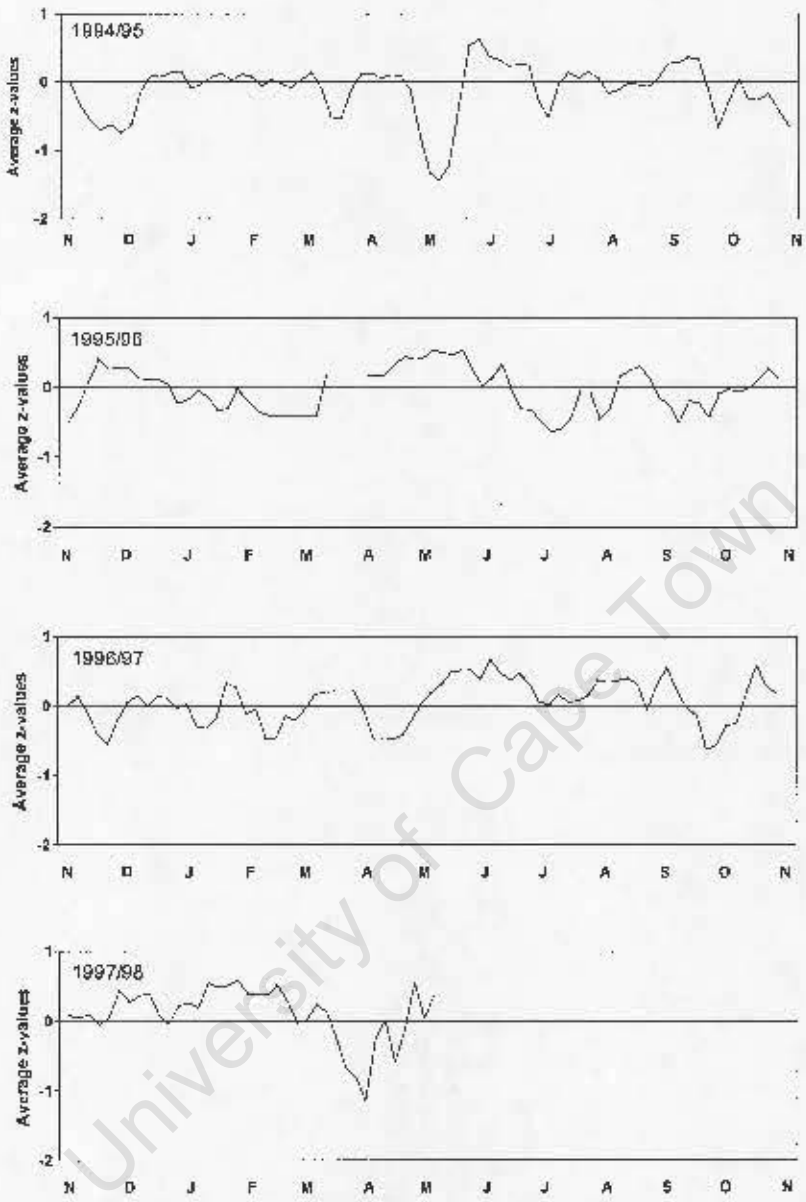

Figure 3.17 Average z-values (standardised growth rates) of all African Penguin chicks per five day interval per year at Dassen Island, November 1994-May 1998. Positive deviations represent above average growth, and negative deviations below average growth for a specific mass. Every alternate month is displayed on the x-axis. For further details see Chapter Five. Adapted from Figure 5.8.

Appendix 3.1 Definition of Weeks used to obtain the seasonal pattern of moult for African Penguins at Dassen Island

Week	Dates
1	1 July - 7 July
2	8 July - 14 July
3	15 July - 21 July
4	22 July - 28 July
5	29 July - 4 August
6	5 August - 11 August
7	12 August - 18 August
8	19 August - 25 August
9	26 August - 1 September
10	2 September - 8 September
11	9 September - 15 September
12	16 September - 22 September
13	23 September - 29 September
14	30th September - 6th October
15	7 October - 13 October
16	14 October - 20 October
17	21 October - 27 October
18	28 October - 3 November
19	4 November - 10 November
20	11 November - 17 November
21	18 November - 24 November
22	25 November - 1 December
23	2 December - 8 December
24	9 December - 15 December
25	16 December - 22 December
26	23 December - 29 December
27	30 December - 5 January
28	6 January - 12 January
29	13 January - 19 January
30	20 January - 26 January
31	27 January - 2 February
32	3 February - 9 February
33	10 February - 16 February
34	17 February - 23 February
35	24 February - 2 March
36	3rd March - 9th March
37	10 March - 16 March
38	17 March - 23 March
39	24 March - 30 March
40	31 March - 6 April
41	7 April - 13 April
42	14 April - 20 April
43	21 April - 27 April
44	28 April - 4 May
45	5 May - 11 May
46	12 May - 18 May
47	19 May - 25 May
48	26 May - 1 June
49	2 June - 8 June
50	9 June - 15 June
51	16 June - 22 June
52	23 June - 30 June

Chapter Four

Comparison of moult patterns of African Penguins *Spheniscus demersus* at Robben and Dassen Islands

Comparison of moult patterns of African Penguins *Spheniscus demersus* at Robben and Dassen Islands

ABSTRACT

Dassen and Robben Islands are approximately 50km apart, and currently support the largest and third largest populations of African Penguins *Spheniscus demersus*, respectively. At both islands, moult was the most synchronised and seasonal activity of the annual cycle. The main difference in moult phenology between the two islands was the degree of synchronisation. The peak moult period at Dassen Island was broader (less synchronous) than at Robben Island, probably as a result of the more prolonged nature of breeding activities prior to moult at Dassen Island, and the larger size of the population compared with Robben Island. The greater availability of burrow and boulder nests at Dassen Island may have allowed penguins there to continue breeding through the hot summer months, thus facilitating a more extended breeding period than at Robben Island. At both Dassen and Robben Islands juvenile penguins moulted less synchronously than adults. The pattern of moult for juvenile penguins was less synchronous at Dassen Island than at Robben Island, presumably due to the more prolonged nature of breeding activities at Dassen Island. Inter-annual variation in moult phenology was similar at Robben and Dassen Islands. Island-level moult phenology was more synchronous in the year following the *Treasure* spill than was the case after the *Apollo Sea* spill. This was attributed to the larger number and proportion of birds that were affected by the *Treasure* spill, and thus the greater impact on the overall moult pattern. The temporal duration of the disruption to moult patterns was also greater following the *Treasure* spill, especially at Robben Island. Moult counts provide a relatively reliable method of estimating the size of the adult population at Robben Island, but not at Dassen Island, where the large number of birds moulting away from the shoreline results in the population size being significantly underestimated. Although the number of active nest sites continued to increase up until 2004 at both islands, the numbers of adult moulters counted declined by 55% between 2003 and 2005 at Robben Island, and by 50% between 2002 and 2005 at Dassen Island. The decrease in the number of moulters coincided with a decreased availability of food in the region.

INTRODUCTION

African Penguins *Spheniscus demersus* moult annually (Randall & Randall 1981, Chapter Three). Moult is the most synchronised component of the annual cycle, and is also the most seasonal, taking place at the same time of the year at each colony, but

showing variation in timing between colonies (Underhill & Crawford 1999, Crawford *et al.* 2006a, Kemper 2006, Chapter Three). At South African colonies, most penguins moult from September to January, with a tendency for penguins to commence moult earliest at Bird Island (33°50'S, 26°17'E) in the Eastern Cape, and to moult latest at Dassen (33°25'S 18°05'E) and Robben (33°48'S, 18°23'E) Islands, in the Western Cape (Crawford *et al.* 2006a). At Namibian colonies, most adult penguins moult in April and May, whereas most juveniles moult between November and January (Kemper & Roux 2005, Kemper 2006).

In African Penguins, the distinctive feather-shedding phase of moult lasts on average 12.7 days (Randall *et al.* 1986b). Two-weekly counts of feather-shedding adult penguins over a year should therefore be of different individuals, and the sum of these counts should represent the size of the adult population (Randall *et al.* 1986b). This census method has been widely applied to estimate the size of the adult population for breeding colonies and regions (Randall *et al.* 1986b, Crawford *et al.* 1990, 1995c, 1999, 2000a, Crawford & Boonstra 1994, Kemper *et al.* 2001). It has also been used, together with nest counts, to estimate the proportion of adult penguins which abstain from reproduction each year (Crawford *et al.* 1999), a factor which can have a major influence on population dynamics in long-lived species (Jenouvrier *et al.* 2005).

Juvenile African Penguins have a distinguishable plumage from adults. They undergo their first moult and attain their adult plumage from 12 to 23 months after hatching (Randall 1989, Kemper & Roux 2005). At most South African colonies, the seasonal pattern of moult for juvenile penguins is similar to that for adults, although extending for longer, often with a secondary peak (Underhill & Crawford 1999, Crawford *et al.* 2006a). Counts of juvenile penguins moulting at colonies represent those birds which have survived the post-fledging period, and have therefore been used as an index of recruitment into the adult population (Crawford *et al.* 1995c, 2000a, 2007).

The synchronised pattern of moult of adult African Penguins was disrupted at both Robben Island and Dassen Islands following the *Apollo Sea* oil spill in June 1994 (Underhill & Crawford 1999, Chapter Three), and after the *Treasure* oil spill in June 2000 (Hemming 2001, Crawford *et al.* 2006a, Chapter Three).

In this chapter, I compare the patterns of moult of adult and juvenile African Penguins at Robben and Dassen Islands over a 10-year period for Dassen Island and a 17-year period at Robben Island. I determine the year-to year variation in the timing and synchrony of moult at these colonies, and explore the factors that might contribute to the inter-colony differences. I also investigate the usefulness of moult counts as population monitoring tools at both colonies.

METHODS

African Penguins in the feather-shedding phase of moult have been counted once every two weeks at Robben Island since 1988 (Crawford *et al.* 1995c, 2006a, Underhill & Crawford 1999), and at weekly intervals at Dassen Island from November 1994 until July 1999, and at two-weekly intervals from August 1999 until September 2006 (Chapter Three). Counts of moulting penguins were restricted to those birds along the shoreline, because this is where most penguins moult (Crawford & Boonstra 1994, but see Chapter Three). Adult and juvenile moulters were counted separately. At Dassen Island, the number of non-moulting juvenile birds along the shore was also counted from November 1994 until October 1998. Gaps in the data were filled by linear interpolation between actual counts to estimate the number of birds moulting each day (Underhill & Crawford 1999). These daily estimates were summed in seven day periods starting 1 July of each year and divided by 12.7, the average duration of the feather-shedding period (Randall *et al.* 1986b), to estimate the number of birds reaching the mid-point of the feather-shedding phase of moult in each week. The number of penguins moulting over each 12-month period from 1 July– 30 June was similarly estimated. Each annual moult period (July–June) therefore spans two calendar years. For comparative purposes, these 12-month periods were converted into years, by using the year in which the peak moult period (November–December) occurred (Crawford *et al.* 2006a, Chapter Three). For example, birds moulting during the period July 1988 to June 1989 are treated as having moulted in 1988.

The average pattern of moult for both adult and juvenile penguins was calculated for the period 1988/89–2005/06 for Robben Island and 1995/96–2005/06 for Dassen Island by summing the weekly totals over all years, and representing these as the percentage of

birds moulting in each week (Underhill & Crawford 1999). Week 1 was defined as the week beginning July 1. In order to quantify the departure of a particular year's moult pattern from the average pattern, the expected number of moulters per week was calculated by multiplying the average proportion of moulters per week by the estimated total number of birds that moulted during that year. For each year, the weekly deviation from the average pattern was calculated as the difference between the observed and expected number of birds moulting per week. The deviation in numbers was divided by the total number of birds that moulted in that year and multiplied by 100 to provide a standardized percentage deviation from average for each week of each year.

Because counts of moulting penguins were initiated in November 1994 at Dassen Island, the number of birds moulting from July to October 1994 (largely the pre-moult period) was estimated by multiplying the percentage differences between the counts from November to June for the 1994/95 and 1995/96 seasons by the mean proportion of birds moulting from July to October. This adjustment comprised 1 520 adult penguins (12.9% of the total that moulted in the 1994/95 season) and 80 juveniles (5.1% of the total for the 1994/95 season). These adjustments were used only to estimate the total numbers of adult and juvenile moulters for the 1994/95 season, and not to calculate the average pattern or percentage deviation from this pattern for the 1994/95 season.

Counts of active nest sites of African Penguins have been conducted at Dassen and Robben Islands since the late 1980s (Marine and Coastal Management, unpubl. data). Most counts were conducted from February to September each year (Crawford *et al.* 1990, 1995b). At Robben Island, where more than one count was made in some years, the highest count was assumed to represent the breeding population. Counting methods were as described by Shelton *et al.* (1984), Crawford *et al.* (1990) and Wolfaardt *et al.* (2001). A nest site was considered active if it contained eggs or chicks, if it was actively defended by an adult bird, or if there were clear signs of recent nest-building activity. The number of chicks in crèches were divided by two, assuming that a maximum of two chicks hatch from a single pair or nest, to determine the number of nest sites they represented, with remaining numbers taken to represent an additional site. Since 1999, a distinction has been made between currently active nest sites (those with eggs and chicks and/or defended by adults) and potential nest sites (those with signs of recent nest building activity) at Dassen Island. At Robben Island, no distinction was made

between these two categories. Numbers of active nest sites reported for both colonies include the sum of these two categories, unless otherwise stated. I have collated published and unpublished information on the sizes of the breeding population from 1988 (in the case of Robben Island) and 1995 (for Dassen Island) until 2005 and assess how the active nest counts compare with the moult counts at both localities.

RESULTS

Moult patterns of adult African Penguins

The proportion of African Penguins in adult plumage that moulted at Robben Island reached a peak of 9.5% in Week 23, the first week of December (Figure 4.1, see Appendix 3.1 for the dates included in each of the weeks). Fifty-one percent of the birds moulted in a six-week period around the peak, from Week 20 to Week 25. The average pattern of moult for adult penguins at Dassen Island was less synchronized than for birds at Robben Island. In the six-week period around the peak (from Weeks 18–23), 38.4% of all adults were recorded moulting (Figure 4.1). At Dassen Island, the largest proportion of adult moulters (6.9%) was recorded in Week 21, two weeks earlier than the peak for birds at Robben Island (Figure 4.1). The proportion of adult birds moulting per week at Dassen Island remained at a similar level (above 6.5%) until Week 24, beyond the peak moult week for Robben Island birds.

The extent of deviation from the average annual pattern of moult for adult penguins varied from year to year at both Robben and Dassen Islands (Figures 4.2 & 4.3). During the 1992/93 moult season at Robben Island, 5.9% more birds moulted in Week 23, the peak period of moult for adult penguins at Robben Island, than was expected (Figure 4.2). The percentage excess moulters remained positive until Week 27. The deviation in 1992/93 relates to a more synchronous moult during this period (Figure 4.4). In 1994/95, an excess of moulters from Week 15 to Week 20 at Robben Island and a deficit from Week 21 to Week 27, indicates that birds moulted earlier than expected (Figure 4.2). In 1996/97 adult penguins at Robben Island moulted later than expected; in Week 28, 6.5% more birds were recorded moulting than was expected from the average pattern (Figure 4.3). Robben Island adults also moulted later than the average peak in 1998/99. In

2000/01 and to a lesser extent in 2001/02, the peak moult period for adult penguins at Robben Island was earlier than the average pattern (Figure 4.3).

Deviation from the average annual pattern of moult for adult birds at Dassen Island was generally less than at Robben Island. The average pattern of moult was less synchronous at Dassen Island (Figure 4.1) and the year to year variation in the timing and synchrony of moult is built in to this average pattern. The greatest deviation from the average pattern at Dassen Island was in 2000/01, when the peak moult occurred one week earlier than the average peak. There was an excess of adult moulters (i.e. positive deviation) from Week 18 to Week 24, peaking in Week 20 when 4% more adult penguins moulted than was expected (Figure 4.3). This pattern was repeated the following year (2001/02), but the percentage deviation was reduced in extent (Figure 4.3). There was a general coherence in the year-to-year patterns of deviation for adult moulters at Robben and Dassen Islands, although the extent of deviation differed between islands in some years, especially in 1996/97 (Figure 4.3).

The degree of synchrony in the pattern of moult varied between years at both Robben and Dassen Islands. At Robben Island the level of synchrony in moult was similar from 1988/89 to 1993/94, fluctuating more widely thereafter (Figure 4.4). The period in which 60% of adult birds had been recorded moulting ranged from five weeks in 1992/93 to 13 weeks in 2001/02 (Figure 4.4), with a mean of 7.8 weeks (Table 4.1). At Dassen Island the time it took for 60% of the adult birds to moult ranged from nine weeks, in 1998/99, 1999/2000 and 2000/01, to 13 weeks in 2002/03 (Figure 4.4), with a mean of 10.7 weeks (Table 4.1).

Moult patterns of juvenile African Penguins

The average pattern of moult for juvenile penguins at both Robben and Dassen Islands was less synchronized than that of adults (Table 4.1). The patterns were characterised by a main peak in Week 23 at both islands, which coincided with the moult peak for adult birds at Robben Island, and was two weeks later than the peak for adult moulters at Dassen Island (Figures 4.1 & 4.5). At both islands the main peak was followed by a smaller secondary peak, from Weeks 34–37 (Figure 4.5). The pattern of moult for juvenile penguins was more spread out (i.e. less synchronised) at Dassen Island than at Robben Island (Table 4.1, Figure 4.5). The period by which 60% of all juveniles had

been recorded moulting at Robben Island ranged from eight weeks (in 2004/05) to 20 weeks (in 2000/01), with a mean of 13.1 weeks; at Dassen Island, this period ranged from 12 weeks (in 1998/99) to 18 weeks (in 2000/01), with a mean of 15.4 weeks (Table 4.1, Figure 4.6). The variation in the degree of synchronization of moult for the period 1994/95–2005/06 was similar at Robben and Dassen Islands (r_s = 0.69, df = 10, P = 0.0130, Figure 4.6). At both islands, moult was least synchronous in 2000/01 (Figure 4.6).

Deviation from the average pattern of moult varied from year to year (Figures 4.7 & 4.8), and was not always synchronous with the pattern of deviation for adults. In 1994/95 juvenile penguins at Robben Island moulted later than the average pattern (Figure 4.7), in contrast to the earlier moult of adult penguins (Figure 4.2). The extent of deviation from the average pattern of moult was greater for juvenile penguins at Robben Island than at Dassen Island; the patterns of deviation were similar in most years (Figure 4.8). At both islands juvenile penguins moulted earlier than expected in 2000/01, following the *Treasure* oil spill.

At Dassen Island, non-moulting juvenile penguins were observed throughout the year, with a broad seasonal peak from Week 15 to Week 30 (Figure 4.9). The lag between the initial increase in the number of juvenile penguins counted, and the increase in the number of juveniles moulting was approximately seven weeks (Figure 4.9). The pattern of arrival of pre-moulting juveniles was less synchronous than the pattern of moult for juvenile penguins (Figure 4.9).

Numbers of penguins moulting and nest counts

At Robben Island, the number of adult penguins moulting per annual period (July–June) increased from 3 458 in 1988 until 1994, when 7 948 adult penguins were estimated to moult. The rate of increase from the previous year was highest (> 20%) in 1990, 1992 and 1993 (Figure 4.10). In 1995 and 1996, there was a decrease in the number of adult penguins recorded moulting at Robben Island; thereafter (from 1997) there was a rapid increase in the number of adult moulters, reaching a maximum of 55% for the period 1996–1997, up until 2001 (Figure 4.10). After 2003 the number of adult moulters at Robben Island declined, especially from 2004–2005 (Figure 4.10). In 2005 a total of 7 768 adult African Penguins were estimated to moult at Robben Island, the lowest

number since 1996, when 5 608 adult penguins were estimated to moult. The number of juvenile penguins moulting annually at Robben Island increased gradually (2–5%) from 1988–1990 (Figure 4.10). There was a substantial increase (75%) from 1990 to 1991; numbers remained relatively stable thereafter, with a slight reduction in 1994 and 1995. The number of juvenile moulters increased rapidly again in 1996, in contrast to the pattern for adults, and continued to increase up until 1998 (Figure 4.10). Numbers increased again in 2001, when the estimated number of juvenile moulters reached a maximum of 3 921 birds. From 2001 to 2005 the number of juvenile penguins moulting per 12-month period declined by 32% (Figure 4.10).

The number of adult penguins moulting along the shoreline at Dassen Island per year remained stable from 1994–1996 (range = 12 360–12 953 birds), followed by a rapid increase until 1999. The number of adult moulters then remained relatively stable until 2001, and declined thereafter (Figure 4.11). The number of juvenile penguins moulting per annual period at Dassen Island increased from 1 578 birds in 1994 to 8 462 in 1999; the numbers of juvenile birds moulting at Dassen Island were largest in 1998, 1999 and 2001 (Figure 4.11). After 2001, the number of juvenile moulters declined to 2 184 birds in 2005. In 2005, there were more juvenile birds moulting at Robben Island than at Dassen Island. However, in all other years between 1994 and 2004, the number of juvenile penguins moulting at Dassen Island was between 1.12 (in 2003) and three times (in 1999) the number of juveniles moulting at Robben Island. Over the entire period for which counts were conducted at Dassen Island (1994–2005), the numbers of juvenile penguins moulting there were correlated with counts of juvenile moulters at Robben Island ($r = 0.64$, df = 10, $P = 0.025$).

There was a general increase in the number of nest sites counted at both Robben and Dassen Islands during the course of the respective study periods (Figures 4.12 & 4.13). The maximum counts of active nests sites, comprising 8 524 and 24 971 for Robben and Dassen Islands respectively, were obtained in 2004. The number of adult penguins moulting per 12-month period and the maximum nest count of the preceding period were correlated at Robben Island ($r = 0.83$, df = 16, $P < 0.001$, Figures 4.12 & 4.14), but not at Dassen Island ($r = 0.35$, df = 10, $P = 0.27$, Figures 4.13 & 4.14). The estimates of the number of adult moulters were greater than the annual nest counts obtained in the preceding breeding period by a factor that ranged between 1.09 (in 2005) and 4.07 (in

1988) at Robben Island (Table 4.2). At Dassen Island the ratio of adult moulters to active nest sites ranged from 0.50, in 2005, and 1.96, in 1998 (Table 4.2). The mean ratio of adult moulters to active nest sites was 2.72 (SD = 0.82, n = 18) at Robben Island, and 1.27 (SD = 0.44, n = 12) at Dassen Island.

The proportion of the total active nest count at Dassen Island made up of currently active nests, as opposed to recently used or potential nests, remained above 80% from 1999 until 2002 (Table 4.3). Thereafter this proportion declined steadily until the end of the study. In 2006, the last census of the study period, currently active nest sites made up 40% of the total count (Table 4.3).

DISCUSSION

Trends in the African Penguin colonies at Robben and Dassen Islands

Dassen and Robben Islands currently support, respectively, the largest and third largest colonies of African Penguins globally, and are the two largest colonies in the Western Cape Province (Crawford *et al.* 2001, du Toit *et al.* 2004, Underhill *et al.* 2006, MCM unpubl. data). These islands are only 50km apart, so are likely to be similarly influenced by regional variables, such as fluctuations in food supply (Petersen *et al.* 2006). Although trends in the number of African Penguins at these colonies have been similar over the last 10–15 years (Underhill *et al.* 2006), the historical trends in these two colonies have been markedly different. Dassen Island is a long established colony. The number of adult-plumaged birds was estimated to be about 1.45 million in 1910 (Shannon & Crawford 1999). Numbers dropped to about 30 000 birds in the early 1990s probably as a result of reduced food availability in the region (Crawford *et al.* 1995b, Crawford 1998), but increased substantially thereafter, especially between 1997 and 2001 (Wolfaardt *et al.* 2001, Underhill *et al.* 2006). This coincided with a substantial increase in the biomass of Sardine *Sardinops sagax* and Anchovy *Engraulis encrasicolus* in the region (Barange *et al.* 2004). The number of nest sites counted in 2004 represents the largest number of African Penguin nests recorded at Dassen Island since the initiation of direct census methods in 1979 (Shelton *et al.* 1982, 1984, Crawford *et al.* 1990, Underhill *et al.* 2006). By contrast, the penguin colony at Robben Island became extinct sometime before 1800 (Westphal & Rowan 1971, Brooke 1983), and

was recolonised by African Penguins in 1983 (Shelton *et al.* 1984, Crawford *et al.* 1995c). Numbers of African Penguins breeding at Robben Island increased from nine pairs in 1983 to over 2 000 pairs in 1992 (Shelton *et al.* 1984, Crawford *et al.* 1995a). Thereafter there was rapid growth of the colony, both in terms of its spatial extent and the number of breeding birds, until 2004 (Crawford *et al.* 1999, Underhill *et al.* 2006).

Season of moult

Moult is the most synchronised seasonal activity in the annual cycle of African Penguins (Randall & Randall 1981, Randall *et al.* 1986b, Randall 1989, Crawford *et al.* 1995c, Chapter Three). As was found in earlier studies (Underhill & Crawford 1999, Crawford *et al.* 2006a), there was a distinct peak in the timing of moult in early December for both adult-plumaged birds and juveniles at Robben Island. At Dassen Island, the peak moult period started earlier but was broader (less synchronised) than at Robben Island.

The difference in the synchrony of moult at these two colonies probably relates to breeding activities prior to moult and the larger size of the breeding population at Dassen Island. During this study, African Penguins at Dassen Island bred almost continuously, with peaks in breeding activities, but without an obvious seasonal pattern (Chapter Three). Although African Penguins at Robben Island also have a protracted breeding season, the breeding cycle tends to be more seasonal than is the case at Dassen Island (L.G. Underhill pers. comm.). Few penguins occupy nest sites in November and December whereas in some years at Dassen Island breeding activities within some sub-colonies peak in these months (Chapter Three). The number of active nest starts to increase from January, and reaches a peak in May, and remains at a high level until September (Crawford & Boonstra 1994, Crawford *et al.* 1995b). The seasonal pattern at Robben Island lags about one month behind the annual cycle described for African Penguins at St. Croix Island (33°48'S, 25°46'E) in the Eastern Cape (Randall & Randall 1981, Randall 1989), but is otherwise similar. The more prolonged nature of the "breeding season" at Dassen Island is likely the cause of the less synchronous moult season than at Robben Island. The larger size of the breeding population at Dassen Island, the larger area occupied by breeding birds and the larger number of distinct sub-colonies which differ in their breeding phenology (Chapter Three) probably contribute towards the protracted and erratic nature of the "breeding season", and consequently the lower level of moult synchrony, at Dassen Island. Synchronisation of breeding within

sub-colonies and lack of breeding synchrony between sub-colonies has been documented on Halifax Island (26°39'S, 15°04'E), Namibia (Kemper 2006).

At Dassen Island, long inter-moult intervals by individual penguins were generally the result of prolonged breeding activities prior to moult (Chapter Three). By contrast, in most years some African Penguin adults at Robben Island abandon their nests relatively synchronously in November and December (R.J.M. Crawford and T.M. Leshoro pers. comms). It is presumed that these are birds that initiated late breeding attempts and deserted their chicks in order to moult (Parsons & Underhill 2004, Underhill *et al.* 2006). This behaviour has also been recorded at Dyer Island (Parsons & Underhill 2004, L. J. Waller *in litt.*), but has not been observed at Dassen Island (pers. obs, J. Visagie *in litt.*). This provides further support for the more protracted nature of the "breeding season" at Dassen Island.

Differences in penguin nesting habitats between Dassen and Robben Islands may be one of the reasons for the more protracted period of breeding by African Penguins prior to and into the peak moult period at Dassen Island relative to Robben Island. At Dassen Island, over 90% of penguins breed in the shelter of burrows, boulders or compact *Tetragonia fruticosa* shrubs (unpubl. data). At Robben Island, the majority (97%) of penguins nest under Manatoka (*Myoporum insulare*) or Rooikrans (*Acacia cyclops*) trees and bushes (Crawford *et al.* 1995c). Although the Manatoka and Rooikrans trees and shrubs afford penguin nests on Robben Island some shade and protection from the high ambient temperatures and more intensive solar radiation during the summer months, they do not provide as much cover as most burrow, boulder and *Tetragonia* nests do at Dassen Island (pers. obs), and therefore may not provide the same degree of protection from heat stress. Burrow nests have been shown to reduce the effects of high ambient temperatures (Frost *et al.* 1976b), thereby providing a major advantage in terms of increased breeding success for nesting African Penguins (Frost *et al.* 1976a, Williams & Cooper 1984, Seddon & van Heezik 1991, Murison 1998), which, with other *Spheniscus* penguins, seem "over-insulated" for the terrestrial component of their lives (Boersma 1976, Frost *et al.* 1976b, Siegfried 1982, Davis 1993, Davis & Renner 2003). The value of burrow nests has also been highlighted for other *Spheniscus* species. At Punta San Juan (15°22'S, 75°12'W) in Peru, burrow nests of Humboldt Penguins *Spheniscus. humboldti* were more successful than exposed nests in areas where the substrate

comprised guano (Paredes & Zavalaga 2001). At Punto Tombo (44°02'S, 65°11'W) in Argentina, covered nests of Magellanic Penguins *Spheniscus magellanicus* were more successful than surface nests, and burrows generally provided more cover than bush nests (Boersma *et al.* 1990, Stokes & Boersma 1998). Characteristics other than the degree of cover may also be important. Even among burrow and bush nests of similar cover, burrows may be advantageous due to their more favourable thermal environment for egg and especially chick survival (Siegfried 1982, Frere *et al.* 2002).

The greater availability of burrow nests at Dassen Island would therefore allow penguins to continue breeding through the hotter summer months as long as there was sufficient food to do so. Indeed, controlling for other explanatory variables, burrow nests tend to be more successful in summer because of the lower probability of burrow collapse and flooding due to heavy rain (La Cock 1988, Seddon & van Heezik 1991). It is possible that the large scale abandonment of nests at Robben and Dyer Islands may be a result of heat stress early in summer, rather than the birds deserting nests to moult, or a combination of these factors. Large-scale abandonment of nests due to high (above 30°C) ambient temperatures has been reported for African Penguins at Halifax Island (26°39'S, 15°04'E) in Namibia (Kemper 2006), and at St. Croix Island in Algoa Bay, especially in January and February (Randall 1983). In December 1979 large numbers of penguin chicks were deserted and died as a result of heat stress at Marcus Island (33°02'S, 17°58'E) (A.J. Williams pers. comm.). At all of these localities, the substrate is currently unsuitable for burrow nesting, and most birds' nests are fully exposed to solar insolation.

The moult phenology of adult penguins at Dassen Island is markedly more synchronous than the pattern of breeding (Chapter Three). The timing of moult of adult penguins at Dassen Island, and other colonies in the Western Cape, appears to have evolved to coincide with the relatively predictable availability of food over the Agulhas Bank from September to February (Chapter Three). During this period Sardine and Anchovy congregate there to spawn (Hampton 1987, Crawford 1998, Crawford *et al.* 2006a, Chapter Three). The Agulhas Bank is more than 200km away from Dassen Island, out of reach for breeding, and especially chick-rearing penguins (Wilson & Wilson 1995). However, birds in pre-moult condition are not constrained to return to the breeding colony, and can travel greater distances to reach the spawning fish over the Agulhas

Bank from September to February. Within the September to February time constraint, African Penguins at Dassen Island generally appear to be able to delay moult until the completion of their breeding attempt. In addition, a small percentage of penguins moult outside of the September to February period (Chapter Three). Due to the extended and less synchronous pattern of breeding at Dassen Island (Chapter Three), some adult penguins commence moult earlier than is the case at Robben Island and others much later. Penguins breeding towards the end of the year at Robben Island seem less able to delay moult to complete their breeding attempt, which may relate to the reduced ability of Robben Island nests to afford sufficient protection against high ambient temperatures and heat stress.

The more continuous nature of breeding at Dassen Island probably also explains the broader peak in the pattern of moult for juvenile penguins than at Robben Island. At both islands, the major peak in early December is followed by a secondary peak in February and March. Although chicks fledge throughout the year (Cooper 1980, Wilson 1985, Whittington *et al.* 1996, Chapters Three and Five), moult of juvenile penguins is seasonal, broadly coinciding in South Africa with the moult period for adult penguins, although of longer duration. As a result juvenile African Penguins do not undergo their first moult at a specific age. Indeed, juveniles have been recorded moulting from 12 to 23 months after hatching (Randall 1983, 1989, Kemper & Roux 2005). Kemper & Roux (2005) have suggested that juvenile penguins which fledge over a 12 month period moult during one of two separate moult seasons. Those that fledge during the austral summer and early autumn mostly moult during the following summer moult peak at the age of about one year (Kemper & Roux 2005). Those that fledge in late autumn, winter and spring are too young to moult in their first summer, and most delay their moult until the following summer, when they would generally be much older than one year. The birds that moult in the first summer after hatching tend to moult later in the moult season, and those that moult during the following season moult earlier (Kemper & Roux 2005). The primary and secondary moult peaks of juvenile penguins at Robben and Dassen Islands could therefore comprise these two groups of birds: the older birds that "missed" the first summer moult season making up the primary peak in December, the secondary peak being made up of younger birds that were able to fit in their first moult in the year following their hatching. At Dassen Island a greater proportion of juveniles moult during the secondary peak (i.e. the primary and secondary moult peaks are more distinct) than

is the case at Robben Island. This again highlights the greater seasonal spread of breeding activities by penguins at Dassen Island. These hypothesized patterns should be investigated further.

Inter-annual variation in the timing and synchrony of moult

Inter-annual variation in moult phenology was largely similar at Robben and Dassen Islands. The large deviations indicating a later moult in the 1995/96 season for both adult and juvenile moulters at Robben Island were attributed to observer error by Underhill & Crawford (1999). In most other years adult penguins at Robben Island tended to moult later than the average seasonal pattern. The exceptions were in 1994/95, 2000/01 and 2001/02, and to a lesser extent in 2004/05 and 2005/06, when moult was earlier than expected from the average pattern. Later moult probably relates to the timing and outcome of breeding activities prior to the moult (Randall & Randall 1981, van Heezik & Davis 1990, Weimerskirch *et al.* 1992, van Heezik *et al.* 1994, 1995), and highlights further the impact of the irregular breeding cycle on the timing and synchrony of moult in African Penguins. However, the outcome of breeding attempts could also result in an earlier moult. For example, if penguins were to experience high breeding failure due to poor food availability (e.g. Boersma 1976, Duffy *et al.* 1984, Crawford & Dyer 1995, Crawford 1998) or inclement weather (e.g. Randall 1983, Randall *et al.* 1986a), they may be in a position to moult earlier.

The earlier moult in 1994/95 at Robben Island and in 2000/01 and 2001/02 at both Robben and Dassen Islands corresponded to the periods following two major oil spills in the vicinity of these islands: the *Apollo Sea* oil spill in June 1994 (Dehrmann 1994, Underhill *et al.* 1999, Underhill & Crawford 1999) and the *Treasure* oil spill in June 2000 (Crawford *et al.* 2000b, Kuyper & Williams 2004, Crawford *et al.* 2006a). In 1994 the peak moult of adult penguins at Robben Island occurred one month earlier than the average pattern. This, together with the loss of synchrony, was attributed to the termination of breeding and the earlier commencement of moult by de-oiled birds, and probably their mates (Underhill & Crawford 1999). Following the *Treasure* spill in 2000 moult of adult-plumaged birds was about two weeks earlier than average at both Robben and Dassen Islands. At Robben Island, the earlier moult was driven by the de-oiled penguins that entered moult before unaffected birds (Hemming 2001, Crawford *et al.* 2006a).

Although the peak moult of adult penguins at Dassen Island in 2000/01 was earlier than average, de-oiled penguins from the *Treasure* spill moulted at a similar time to unaffected birds (Chapter Three). Un-oiled adult penguins that were evacuated from Dassen Island and relocated to Cape Recife (34°02S, 18°30E) in the Eastern Cape moulted later than average in 2000/01. This was probably a consequence of these birds initiating breeding attempts soon after their return to Dassen Island (i.e. "late" in the year), which in turn delayed their moult in 2000/01 (Chapter Three). Although a large number of penguins (12 345) was evacuated from Dassen Island (Chapter Six), the generally later moult of these birds did not drive the pattern in 2000/01 at Dassen Island, and suggests that the moult peak in 2000/01 may have been even earlier were it not for the later moult of the *Treasure* evacuees. It is likely that those penguins that were de-oiled did not commence breeding upon their return to Dassen Island and were thus able to enter moult earlier. The remaining "unaffected" birds, those that were not oiled or evacuated, were nevertheless impacted by the oil spill because the rescue operation, which lasted from 21 June to the end of July 2000, resulted in substantial disturbance to all penguins that were at Dassen Island during this period (pers. obs). The disturbance associated with the rescue operation resulted in the desertion of most nests that were active at the time (pers. obs.). In some areas of the island, breeding activities increased immediately after the rescue operation, while in others they remained at a low level until early in 2001 (Chapters Three and Six). Unaffected birds that delayed breeding until 2001 would, like the de-oiled birds, have been in a position to moult earlier than usual. Unaffected birds that did commence breeding within 2000 were probably able to do so earlier than the evacuated birds because the disruption they experienced was of a shorter duration. Consequently, these unaffected birds would have been able to moult earlier than the evacuated birds.

The impacts of the *Apollo Sea* and *Treasure* oil spills on the moult phenology of adult penguins at both Robben and Dassen Islands differed in two main ways. Firstly, moult was markedly more synchronous after the *Treasure* spill than after the *Apollo Sea* spill, especially at Robben Island. The greater degree of synchrony is probably a result of the much higher proportion of penguins at the two islands (more than four times more birds were affected in the *Treasure* spill, Nel *et al.* 2003), especially Robben Island, that were affected by the *Treasure* spill, and thus the greater impact on the overall moult patterns.

Secondly, the temporal extent of the disruption caused by the two oil spills differed. The moult pattern of adult penguins at Robben Island in 1995/96 (the second season of moult after the *Apollo Sea* spill), was similar to the average pattern (Underhill & Crawford 1999). By contrast, the disrupted pattern of moult was still evident in the second year following the *Treasure* spill (2001/02). This highlights again the more severe and extended nature of the disruption compared with that experienced after the *Apollo Sea* spill. The degree of synchrony in moult was lowest at Robben Island in 2001/02. This was likely due to the impact of the *Treasure* spill on the breeding patterns of the de-oiled adult penguins in 2001 (i.e. the year following the spill). Oil contamination may temporarily suppress breeding activities in some individuals through sub-lethal impacts of oil ingestion (Butler *et al.* 1988, Walton *et al.* 1997, Chapter Two), through the loss of a mate and the time required to form a new pair-bond (Fry *et al.* 1986, Kerley & Erasmus 1987, Giese *et al.* 2000), or due to the disruption of breeding and moult cycles. These impacts likely effect individuals in a variable manner, and so contribute towards a more erratic pattern of breeding, and lower level of moult synchrony. The much higher level of moult synchrony in 2000/01 at Robben Island also suggests that few penguins initiated breeding attempts there until after their first post-oiling moult (i.e. from 2001). Following the *Treasure* spill, more than fourfold more oiled penguins were collected from Robben Island than Dassen Island (Crawford *et al.* 2000b). Although the birds caught at Robben Island were not necessarily all residents at that colony (Underhill *et al.* 1999), the marked difference in these numbers probably explains why the impacts of the *Treasure* spill were less severe and of shorter duration at Dassen Island.

Deviations in the pattern and synchrony of moult of juvenile penguins at Robben and Dassen Islands are likely to be due to a range of factors. African Penguin chicks disperse rapidly away from their natal colony after fledging, generally moving in a clockwise direction along the coast; chicks from the Robben and Dassen Islands would therefore disperse in a northerly direction (Randall *et al.* 1987, Underhill *et al.* 1999, Whittington *et al.* 2005c). These birds generally return as juveniles to their natal colonies, where they undergo moult and attain adult plumage from the age of 12 to 23 months (Randall *et al.* 1987, Randall 1989, Kemper & Roux 2005, Whittington *et al.* 2005c). Not all juvenile penguins moult at their natal colony (Kemper & Roux 2005). This may be part of a mechanism for pre-breeders to immigrate to colonies where conditions are more favourable at the time (Crawford 1998, Crawford *et al.* 2001, Whittington *et al.*

2005b). The timing and synchrony of moult in juvenile penguins at a colony would therefore be influenced not only by factors impacting the breeding pattern and temporal productivity at that colony during the preceding year or two, but would also include factors operating in other areas, sometimes during different periods (e.g. at the colonies from which birds emigrated and/or during the post-fledging migration). In 1994/95 the juvenile penguins moulted later than usual at Robben Island, in contrast to the pattern for adults in the same year. The later moult in 1994/95 was attributed to the abandonment of a large number of nests at Robben Island by March 1993; the subsequent laying of replacement clutches probably resulted in a later than average production of chicks in 1993 (Underhill & Crawford 1999). A small proportion of the penguins contaminated following the *Apollo Sea* spill were juveniles (less than 10% of those released with flipper bands, Chapter Two). It is not known whether these birds moulted in 1994/95 or 1995/96. It is possible that the reduced synchrony of juvenile moult at Robben Island in 1995/96 was partly due to an earlier moult by juveniles that were contaminated in the *Apollo Sea* oil spill the year before.

Juvenile moult was least synchronous at both colonies in 2000/01; moult was also earlier than normal at both colonies during this season. The earlier moult of juveniles corresponded to the adult pattern in the same year, which in turn was attributed to the impact of the *Treasure* oil spill. The proportion and number of contaminated penguins that were juveniles (22% in the case of Dassen Island, Chapter Six) was larger than in the *Apollo Sea* spill, and so it is likely that the disruption of the juvenile moult pattern by the *Treasure* spill was far greater than was the case following the *Apollo Sea* spill. The reduced synchrony of the juvenile moult pattern in 2000/01 contrasts with the high level of synchrony of adult moult in the same year. This points to the influence of additional factors (see above). The correlation between the level of synchrony in juvenile moult at Robben and Dassen Islands, together with the similar patterns of deviation from the average pattern in most years, suggests that juvenile moult at these two colonies is influenced by similar regional or sub-regional variables. Years in which patterns differed probably reflect differences in breeding phenology and success between the two islands. The juvenile phase is the least known component of the demography and life-history of African Penguins, and given its importance for population viability assessments (Whittington *et al.* 2000, du Toit *et al.* 2003, Crawford *et al.* 2007), should receive further attention.

Numbers of penguins moulting in relation to nest counts

Counts of active nest sites provide a measure of the breeding population, but do not account for those birds that are not yet of breeding age (sub-adults), or abstain from breeding in a particular year (e.g. Boersma 1978, 1998a, Cam *et al.* 1998, Crawford *et al.* 1999, Crawford 2003, Cuthbert *et al.* 2003, Chapter Two). Moult counts have been used as a measure of the size of the total adult population for African Penguins (e.g. Randall *et al.* 1986b, Crawford *et al.* 1995b, c, 2000a). Based on a comparison during the late 1970s of the numbers of adult-plumaged birds moulting and the number of active breeding pairs at colonies in Saldanha Bay and at Dassen Island, a factor of 3.53 was used to adjust counts of breeding pairs upwards to estimate the total adult population (Crawford *et al.* 1991). From 1988 to 1993 the number of moulting adults was higher than the maximum counts of active nest sites for African Penguins at Robben Island by a factor of between 2.5 and 3.7 (mean = 3.2) (Crawford & Boonstra 1994). The mean difference between the number of adult moulters and active nest sites for penguins at Robben Island in this study (1988–2005) was 2.72; at Dassen Island the mean difference was 1.27.

The reduction in the size of difference between counts of adult-plumaged moulters and nest sites at Robben Island in this study, may suggest that in at least some of the additional years, an increased proportion of the adult population attempted to breed. However in some years at Robben Island, the total number of adult moulters counted was less than double the maximum count of nest sites in the preceding period. Each active nest represents two adult penguins. Because African Penguins moult annually (Randall & Randall 1981, Chapter Three), the number of adult-plumaged penguins that would be expected to moult in an annual period would be at least twice the number of active nest sites counted in the preceding period. At Dassen Island, the ratio of moulters to nest sites was less than two in every year of the study, and from 2002–2005 was less than one, which means that the total number of adult moulters counted in these periods was less than the count of active nest sites.

These anomalies suggest that counts of penguins moulting along the shoreline significantly underestimate the total adult population, especially at Dassen Island, but may also be the result of inaccurate nest counts. At Dassen Island a substantial number

of penguins moult in burrows and at other nest sites, especially from June to October (Chapter Three). These birds are not included in the coastal moult count figures and probably account for a large portion of the shortfall in the number of adult moulters. It is difficult to quantify the total number of birds that moult in burrows, because the numbers vary seasonally and per area. Applying the mean proportion of burrows containing moulters in each study area per month (Chapter Three) to the total number of burrows counted in the larger study area during the annual census, the estimated number of penguins moulting in burrows in 2001 ranged between 1 610 birds in Area G, and 7 701 birds in Area D, with a total of 21 657 for all the coastal study areas (Areas A–G), slightly more than the total of 21 409 birds that were estimated to moult along the coast in 2001. Of all re-sightings of flipper-banded penguins moulting at Dassen Island, 32% were of penguins moulting away from the coast (Chapter Three). These figures provide rough estimates of the number of penguins that may moult away from the coast, and serve to highlight the proportion of population that may not be accounted for in the coastal moult counts. The closer match between counts of moulting penguins and active nest sites at Robben Island suggests that fewer penguins moult inland than at Dassen Island. However, the reduction in the difference between the number of adult moulters and the number of breeders or nest sites to below a factor of two in 2004 and 2005 indicates that the incidence of inland moulting needs to be investigated in more detail at Robben Island.

Although adult African Penguins generally moult at their breeding colony (Randall *et al.* 1987, Chapter Three), there are records of birds moulting at colonies other than that at which they breed (Crawford *et al.* 2000a, Whittington 2002, Whittington *et al.* 2005c). This further complicates the interpretation of the ratio of moulters to breeders. This finding is supported by the much larger numbers of adult-plumaged penguins recorded moulting at Boulders (34°11'S, 18°27'E) and Stony Point (34°22'S, 18°54'E) in 2000 than would be expected based on the respective sizes of their breeding populations (Hemming 2001). These two colonies are located close to the Agulhas Bank, which is considered to be an important foraging area for pre-moult African Penguins from the Western Cape (Chapter Three). The excess moulters at Boulders and Stony Point may therefore include birds from colonies such as Robben and Dassen Island, which travelled to the Agulhas Bank to fatten up for their moult, and decided to moult in the vicinity rather than returning to their breeding colonies to moult. It is also possible that

some (probably most) of the "non-resident" birds moulting at these colonies are adult-plumaged penguins not yet of breeding age. African Penguins only start breeding from between two and eight years of age (means from a range of studies = 4–6 years) (Randall 1983, Crawford *et al.* 1999, Whittington *et al.* 2005a). Sub-adult penguins and those which abstain from reproduction in a particular year (Crawford *et al.* 1999, Chapter Two) would be less constrained to return to their resident colony and perhaps more likely to moult away from their colony than active breeders.

Crawford *et al.* (1999) assumed that differences between the number of adult penguins moulting and breeding at Robben Island represented the proportion of penguins that bred each year. However, if penguins visit other colonies to moult, or a large number of penguins moult inland and are not included in the estimates of adult moulters, the proportion of penguins estimated to breed using this method would be inaccurate. The proportion of established breeders that abstain from reproduction each year is a critical parameter in population models of long-lived seabirds (Crawford *et al.* 1999, Shannon & Crawford 1999, Jenouvrier *et al.* 2005, Ryan *et al.* 2007). The potential inaccuracies in the use of moult counts to estimate the size of the adult-plumaged population, and the ratio of adult moulters to nest sites to estimate the proportion of the adult population attempting to breed each year should therefore be investigated further through observations of flipper-banded penguins throughout the region.

The number of juvenile penguins moulting at Robben and Dassen Islands each year would be influenced by three main factors: breeding productivity at the respective colonies in the previous two years; the survival rate of first-year birds; and by rates of immigration and emigration to and from the respective colonies. Breeding success and first-year survival are highly variable (Randall 1983, La Cock *et al.* 1987, La Cock & Hänel 1987, Whittington 2002, Hockey *et al.* 2005), and are in turn influenced by a range of factors, especially the availability of food (Crawford *et al.* 1999, 2000a, 2006b, Chapter Five). The correlation between the numbers of juvenile penguins moulting at Robben and Dassen Islands highlight the importance of regional variables, such as food availability, for the recruitment of juvenile penguins into the adult population. At Dassen Island the largest numbers of juvenile moulters were recorded in 1998, 1999 and 2001, when the biomass of Sardine and Anchovy was at a high level (Crawford *et al.* 2006b, Chapter Five). Large numbers of juvenile moulters were also recorded in these years at

Robben Island. From 1988 to 1995, the number of juvenile penguins estimated to have recruited to Robben Island was positively related to the biomass of Anchovy (Crawford *et al.* 1999). The marked reduction in the number of juvenile moulters at Dassen Island in 2002 and 2003 was not recorded to the same extent at Robben Island. This is possibly because of the greater role of immigration at the Robben Island colony (Crawford *et al.* 1999). Although counts of juvenile moulters provide a useful estimate of recruitment into the adult population, they cannot be related directly to future changes in the size of the breeding population. This is because of the wide range of ages at which African Penguins start breeding, presumably reflecting geographical and temporal variations in the availability of food and the potential costs of reproduction (Erikstad *et al.* 1998, Whittington *et al.* 2005a).

The numbers of adult penguins moulting along the coast declined markedly from 2003 to 2005 at Robben Island (55% reduction in numbers) and from 2002 to 2005 at Dassen Island (50% reduction). Surprisingly, the numbers of active nests counted during the course of the respective study periods reached a maximum in 2004 at both colonies, declining slightly in 2005. However, from 2003 to 2006 the portion of the total nest count at Dassen Island made up of potentially active nest sites (i.e. those without adults, eggs or chicks present, but with signs of recent nest building activity) increased to between 35% (in 2003) and 60% (in 2006); it remained below 20% prior to 2003 (Table 4.3). The much higher percentage of potential nests in the total from 2003 to 2006 may reflect changes in the phenology of breeding activities during these years. However, if a large proportion of the potential nests never translated into actual breeding attempts, these figures probably reflect a reduction in the size of the breeding population.

After 1998 there was an eastward shift in the distribution of Sardine (van der Lingen *et al.* 2005, Fairweather *et al.* 2006), eventually leading to a much reduced availability of prey for penguins west of Cape Point, especially after 2002 (Crawford *et al.* in prep.). A decreased abundance of prey is known to influence the proportion of established breeders that do not breed in any given year (Crawford *et al.* 1999), and will thus influence the estimated size of the breeding population through nest counts. However, even if birds abstain from breeding in a particular year, they would still moult. The decline in the numbers of adult moulters at these colonies may be due to the "missing"

birds moulting elsewhere, to an increased level of mortality amongst adult-plumaged penguins, or a combination of these factors.

El Niño events can have devastating consequences for penguins, particularly for Humboldt and Galápagos Penguins *Spheniscus mendiculus*, which are dependent on the Humboldt and Cromwell upwelling systems. These species generally show more extreme and rapid responses to adverse environmental conditions than has been reported for the African Penguin, which is less affected by El Niño events (Duffy *et al.* 1984, La Cock 1986, Boyer & Hampton 2001, Crawford *et al.* 2006c). During El Niño events, upwelling of nutrient-rich, cold bottom water is depressed leading to a reduction in marine productivity and availability of food for penguins and other seabirds (Boersma 1978, 1998a, b, Culik *et al.* 2000, Vargas *et al.* 2006). In the Humboldt upwelling system off Peru, El Niños can cause large scale reproductive failure, deferred breeding and increased mortality for several seabird species, including penguins (e.g. Hays 1986, Boersma 1998b, Schreiber 2002, Simeone *et al.* 2002). Similarly, El Niño events can result in complete reproductive failure and deferred breeding in the Galápagos Penguin, and in extreme years can cause high adult mortality (Anderson 1989, Boersma 1998a, b). The strategy of deferring breeding or abandoning breeding attempts is presumably a mechanism for birds to avoid the potential costs of reproduction when these are likely to be high, thereby safeguarding their own survival. This is also thought to be the case for African Penguins, which have been shown to abstain from breeding or desert nests in periods of reduced availability of food (Crawford & Dyer 1995, Crawford 1998). African Penguins also appear to be able to delay the onset of breeding until feeding conditions become more favourable (Crawford & Dyer 1995). One would therefore expect deterioration in environmental conditions to manifest in reduced breeding effort before it impacts survival, except during extreme events.

There has not been an increase in the number of dead penguins recovered at Robben and Dassen Islands over the last two years (unpubl. data; R.J.M. Crawford pers. comm.), nor an increase in the number of dead flipper-banded penguins reported by members of the public to the South African Bird Ringing Unit (SAFRING) (M. Brooks, *in litt.*). It seems unlikely, then, that the marked decline in the numbers of adult moulters at Robben and Dassen Islands is due to increased mortality. Where these birds would be moulting is uncertain, and should be investigated further. These findings highlight the

need to design and implement regional monitoring programmes in order to understand better the population dynamics of African Penguins at both a local- and regional-scale. These programmes should include the monitoring of year on year survival rates. This would require that researchers are able to recognise individual birds, either through the use of flipper bands, or some other means, and that a sustained effort is directed towards the re-sighting of individually recognisable birds across the species' range.

My results also show that the current use of coastal moult counts do not provide accurate estimates of the adult population at Dassen Island, which is currently the largest African Penguin colony, supporting 34% of the global population (Hockey *et al.* 2005). At Robben Island, coastal moult counts appear to be a more accurate tool to monitor trends in the penguin population. However, the discrepancies between the moult counts and the annual nest counts in 2004 and 2005 indicate that the counts should be used with caution, and that further research should be conducted to quantify the incidence of inland moulting at Robben Island, and to adapt the methodology accordingly. Despite their shortcomings, moult counts remain an important population monitoring tool that may provide insights into population-level changes that are not detected immediately by other population monitoring tools, such as annual nest counts. For example, the reduction in the number of adult moulters at Robben and Dassen Islands was detected prior to the decline in the number of active nest sites at these islands. Moreover, a decline in the number of adult moulters represents a more serious threat to African Penguin colonies than a reduction in the number of active breeders because it indicates that birds have not merely abstained from breeding, but have moved away from their breeding island.

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Table 4.1 The period (weeks) in which 60% of adult and juvenile African Penguins had been recorded moulting at Robben (1988/89-2005/06) and Dassen Islands (1994/95-2005/06). This period is used as an index of synchronization of the moult.

	Adults				Juveniles				
	Mean	SD	Median	*n*	Mean	SD	Median	*n*	Comparison btw. age groups*
Robben Island	7.83	1.86	8	18	13.11	3.55	13.50	18	$P < 0.001$
Dassen Island	10.73	1.42	11	11	15.45	1.69	16	11	$P < 0.001$
Inter-island comparison*			$P < 0.001$				$P = 0.053$		

* Mann-Whitney U test

Table 4.2 Relationship between the estimated number of adult African Penguins moulting along the shoreline each year (July-June) and the maximum count of active nests in the period preceding the moult peak at Robben and Dassen Islands.

	Robben Island			Dassen Island		
Year	No. of adult moulters	No. of active nests	Ratio of Moulters:Nests	No. of adult moulters	No. of active nests	Ratio of Moulters:Nests
1988	3459	849	4.07	nc	nc	
1989	3392	829	4.09	nc	nc	
1990	4730	1278	3.70	nc	nc	
1991	4915	1879	2.62	nc	nc	
1992	6538	2027	3.23	nc	nc	
1993	8002	2176	3.68	nc	nc	
1994	7948	2799	2.84	12360	9389	1.32
1995	6563	2279	2.88	12222	9792	1.25
1996	5608	3097	1.81	12953	9502	1.36
1997	8696	3336	2.61	16296	8651	1.88
1998	9397	3467	2.71	21438	10918	1.96
1999	11765	4399	2.67	25074	15155	1.65
2000	13362	5705	2.34	26095	17042	1.53
2001	16439	6723	2.45	25619	21409	1.20
2002	14737	7252	2.03	22511	22883	0.98
2003	17424	6433	2.71	17592	20319	0.87
2004	12871	8524	1.51	18298	24971	0.73
2005	7769	7152	1.09	11345	22687	0.50

nc = no count

Table 4.3 Counts of currently active and recently used nest sites of African Penguins at Dassen Island. 1999-2006.

Year	Census month	Currently Active*	% of total	Potential/Recently used '	% of total	Total Active#
1999	June	14449	95.34	706	4.66	15155
2000	April	15598	91.53	1444	8.47	17042
2001	April	18193	84.98	3216	15.02	21409
2002	April	18401	80.41	4482	19.59	22883
2003	May	13373	65.82	6946	34.18	20319
2004	May/June	13549	54.26	11422	45.74	24971
2005	May	11105	48.95	11582	51.05	22687
2006	May	5353	40.30	7930	59.70	13283

* Includes nest sites with eggs, chicks and/or defending adults
' Includes nest sites with clear signs of recent nest-building activity
Sum of the Currently Active and Recently Used categories

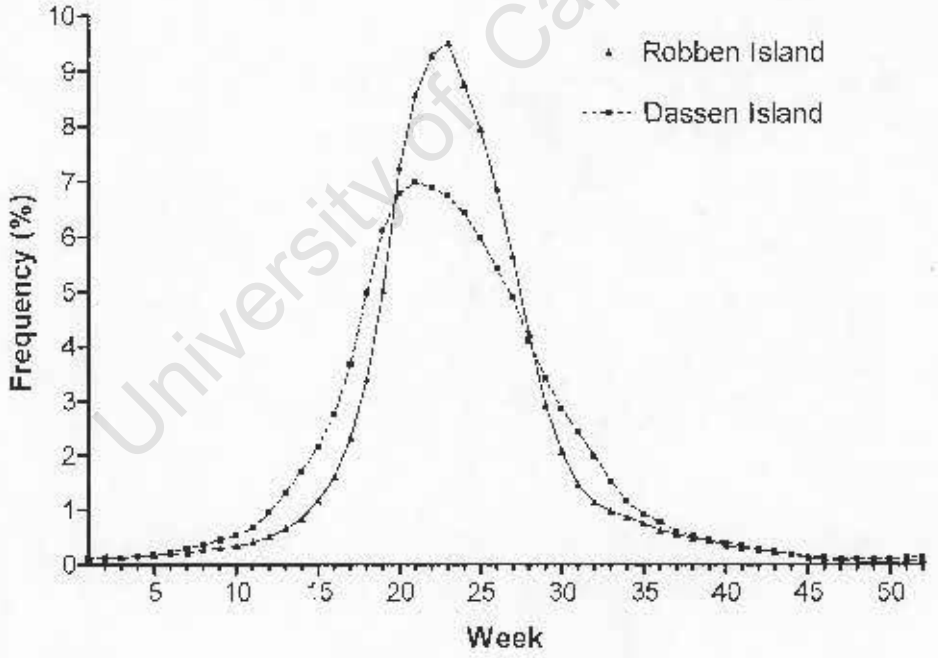

Figure 4.1 Average seasonal pattern of moult for adult African Penguins at Robben and Dassen Islands for the period 1988/89-2005/06 at Robben Island and 1994/95-2005/06 at Dassen Island, expressed as the percentage of birds moulting in each week. Week 1 is the week beginning 1 July.

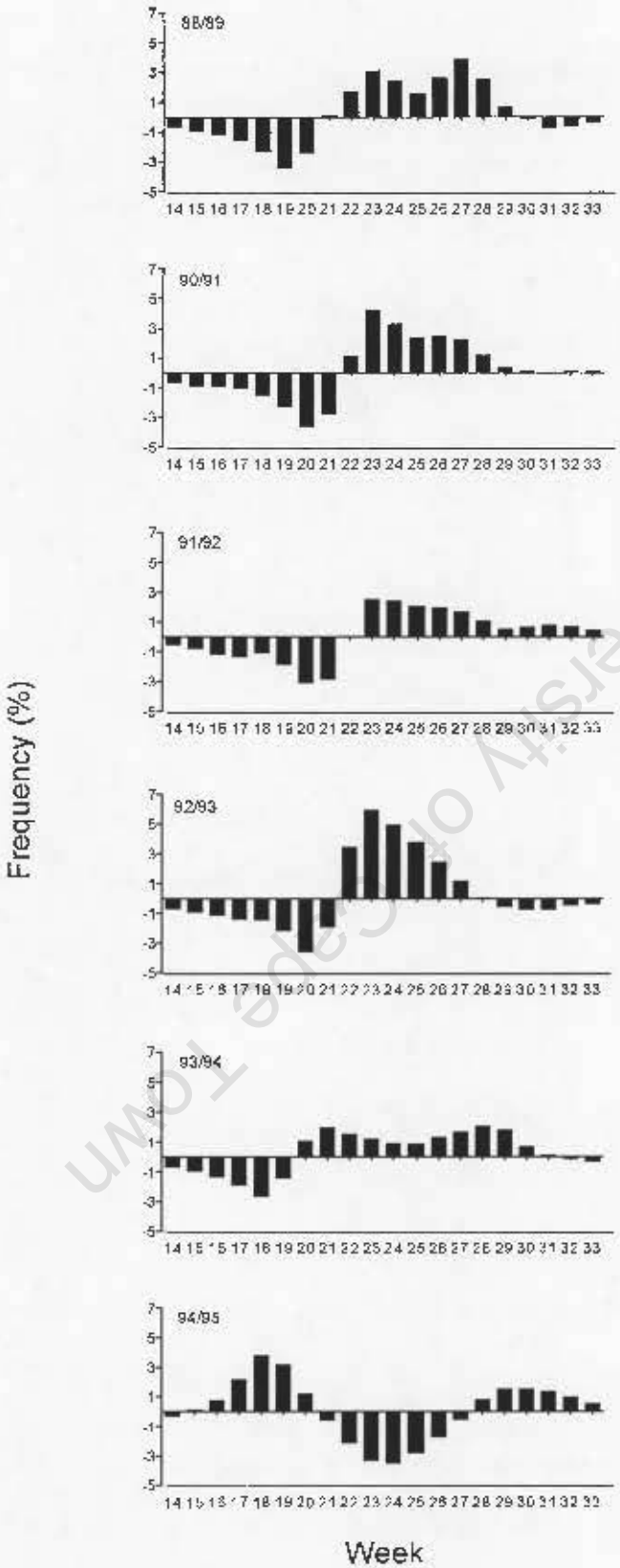

Figure 4.2 Standardized percentage deviation of the proportion of adult African Penguins moulting at Robben Island per week relative to the average annual pattern for the period 1988/89 to 1994/95. Positive deviations indicate more moulters than expected from the average pattern, and negative deviations less moulters. Only the peak moult period, from Week 14 - 33, is included.

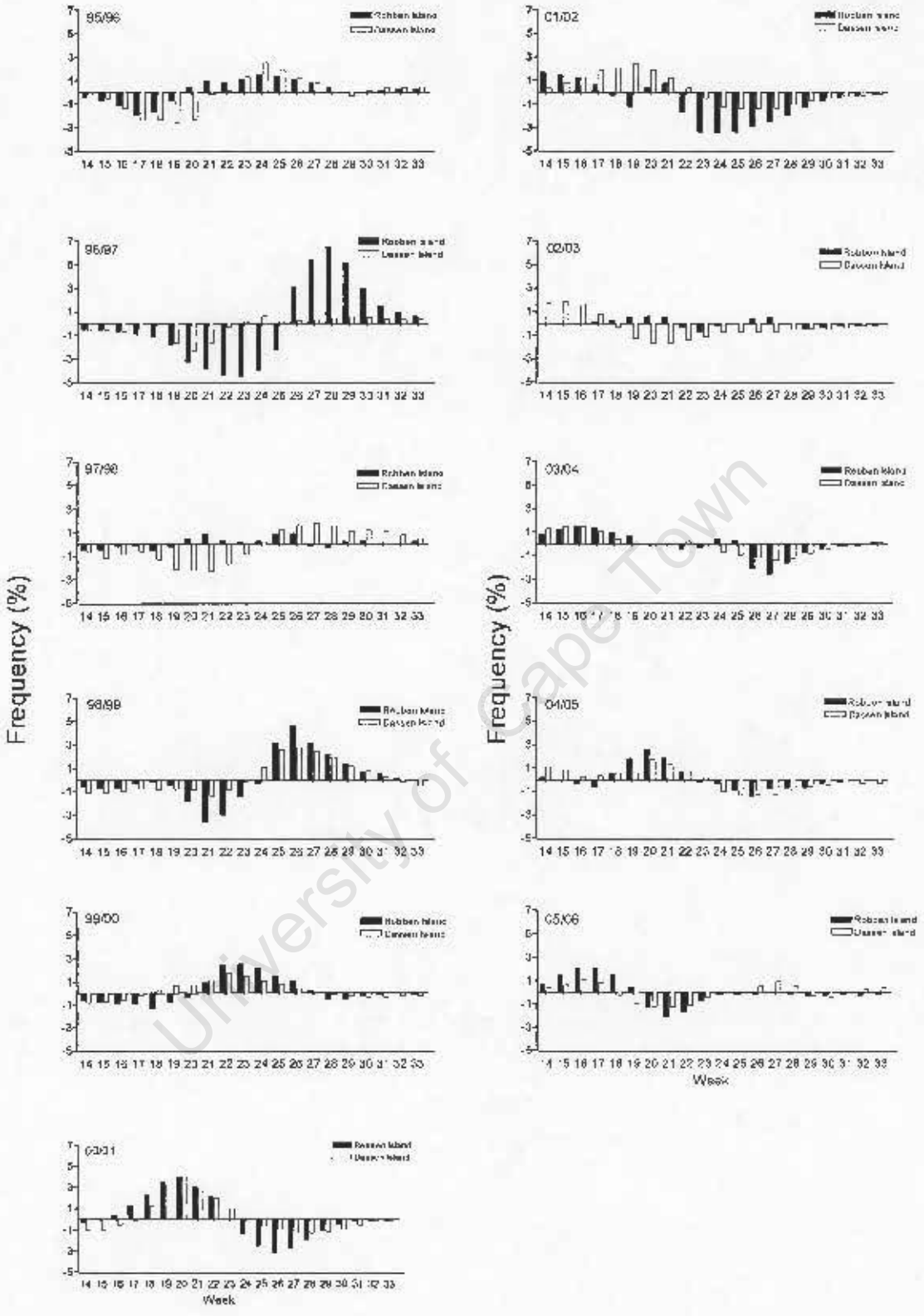

Figure 4.3 Standardized percentage deviation of the proportion of adult African Penguins moulting at Robben and Dassen Islands per week relative to the average annual pattern for the period 1995/96-2005/06. Positive deviations indicate more moulters than expected from the average pattern, and negative deviations less moulters. Only the peak moult period, from Week 14 - 33, is included.

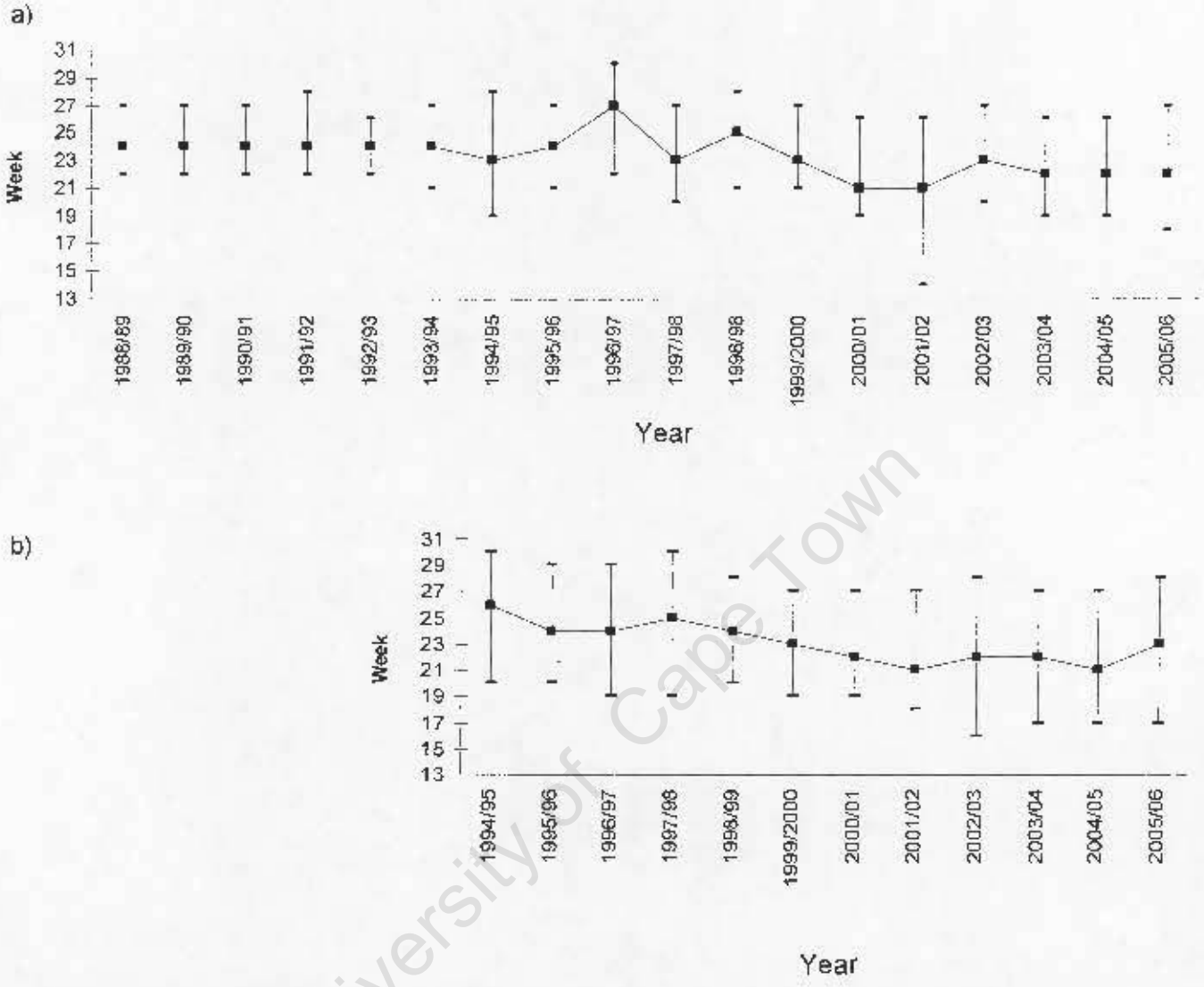

Figure 4.4 Cumulative percentages of adult African Penguins moulting per week at a) Robben Island and b) Dassen Island. The week in which 50% of birds had been recorded moulting is represented by the joined squares. The lower and upper error bars represent the weeks in which 20% and 80% of birds had been recorded moulting respectively.

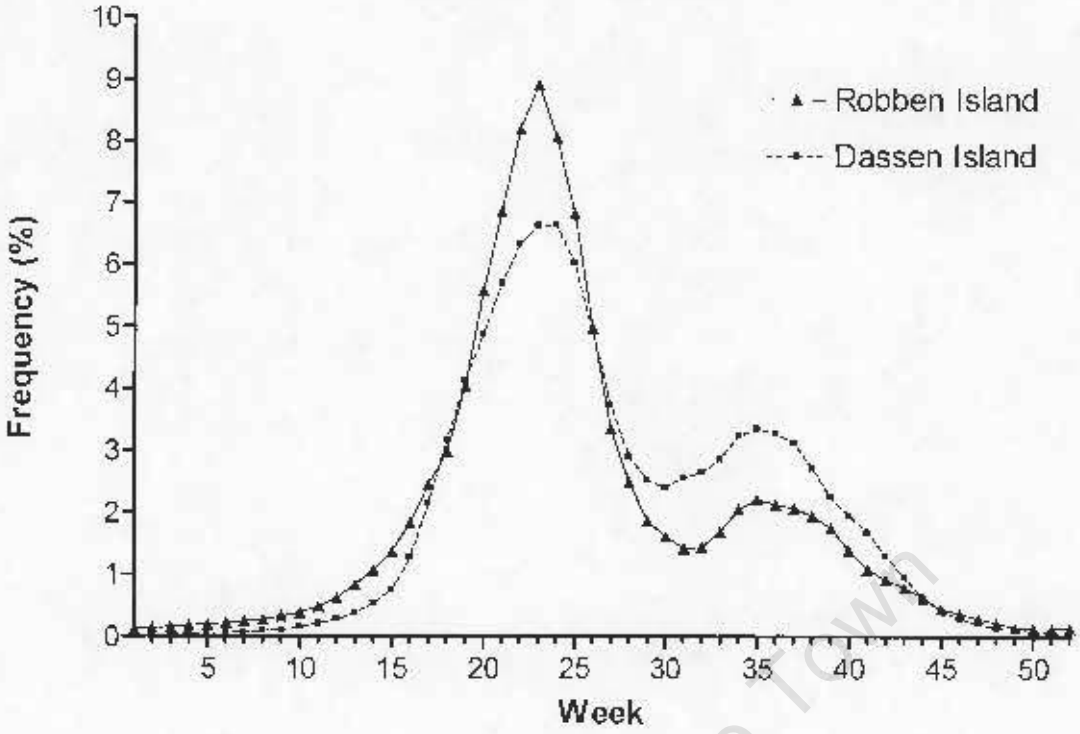

Figure 4.5 Average seasonal pattern of moult for juvenile African Penguins at Robben and Dassen Islands for the period 1988/89-2005/06 at Robben Island and 1994/95-2005/06 at Dassen Island, expressed as the percentage of birds moulting in each week. Week 1 is the week beginning 1 July.

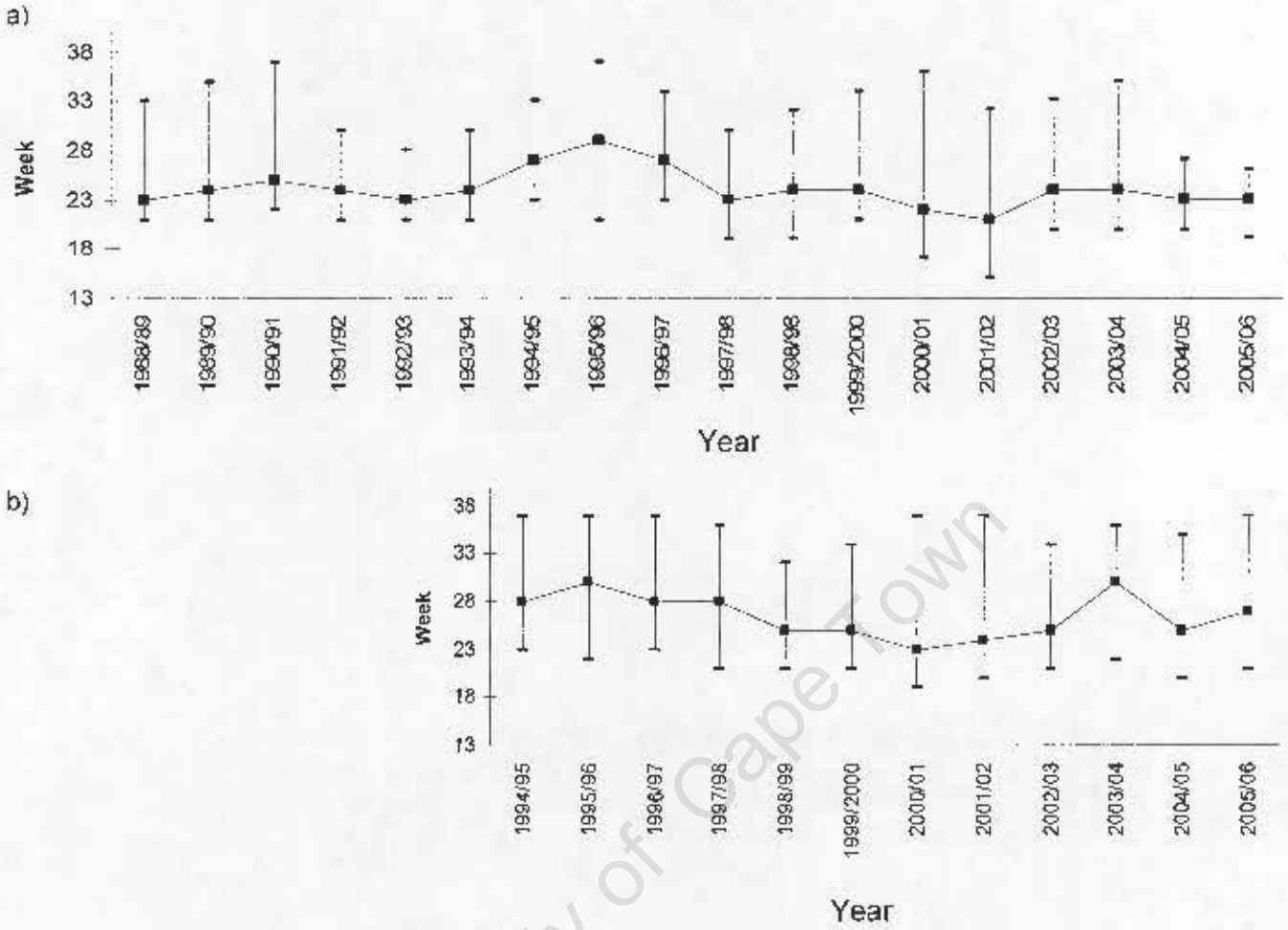

Figure 4.6 Cumulative percentages of juvenile African Penguins moulting per week at a) Robben Island and b) Dassen Island. The week in which 50% of birds had been recorded moulting is represented by the joined squares. The lower and upper error bars represent the weeks in which 20% and 80% of birds had been recorded moulting respectively.

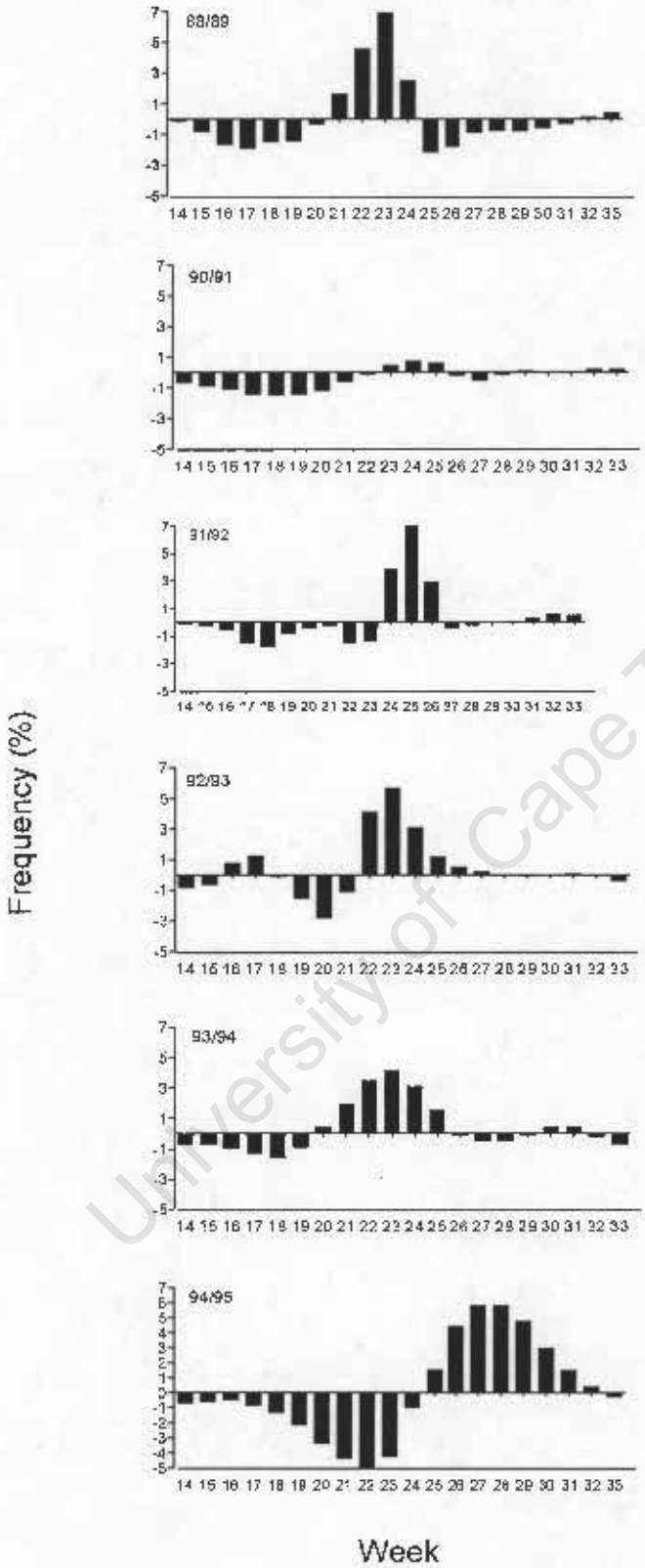

Figure 4.7 Standardized percentage deviation of the proportion of adult African Penguins moulting at Robben Island per week relative to the average annual pattern for the period 1988/89 to 1994/95. Positive deviations indicate more moulters than expected from the average pattern, and negative deviations less moulters. Only the peak moult period, from Week 14 - 33, is included.

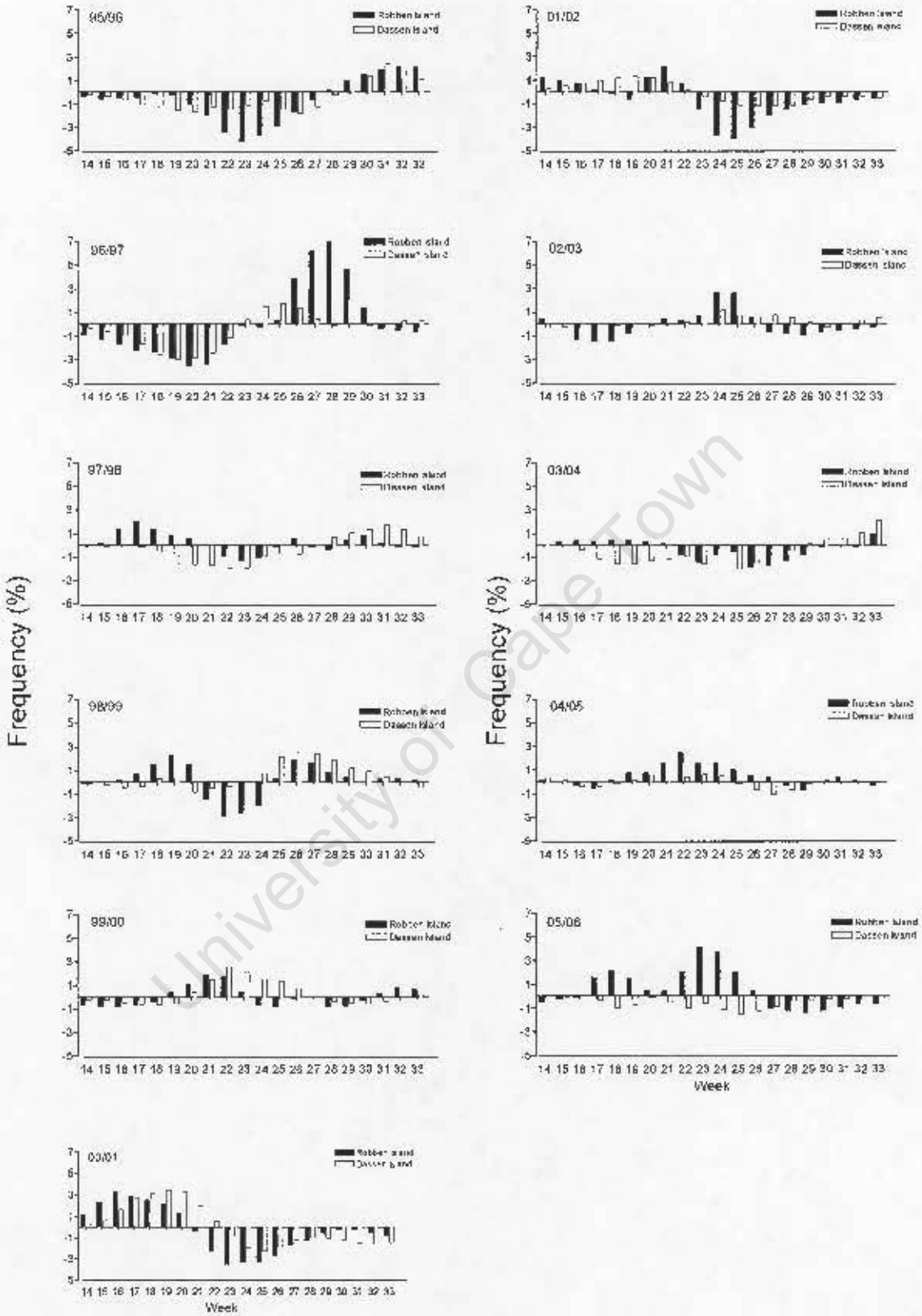

Figure 4.8 Standardized percentage deviation of the proportion of juvenile African Penguins moulting at Robben and Dassen Islands per week relative to the average annual pattern for the period 1995/96-2005/06. Positive deviations indicate more moulters than expected from the average pattern, and negative deviations less moulters. Only the peak moult period, from Week 14 - 33, is included.

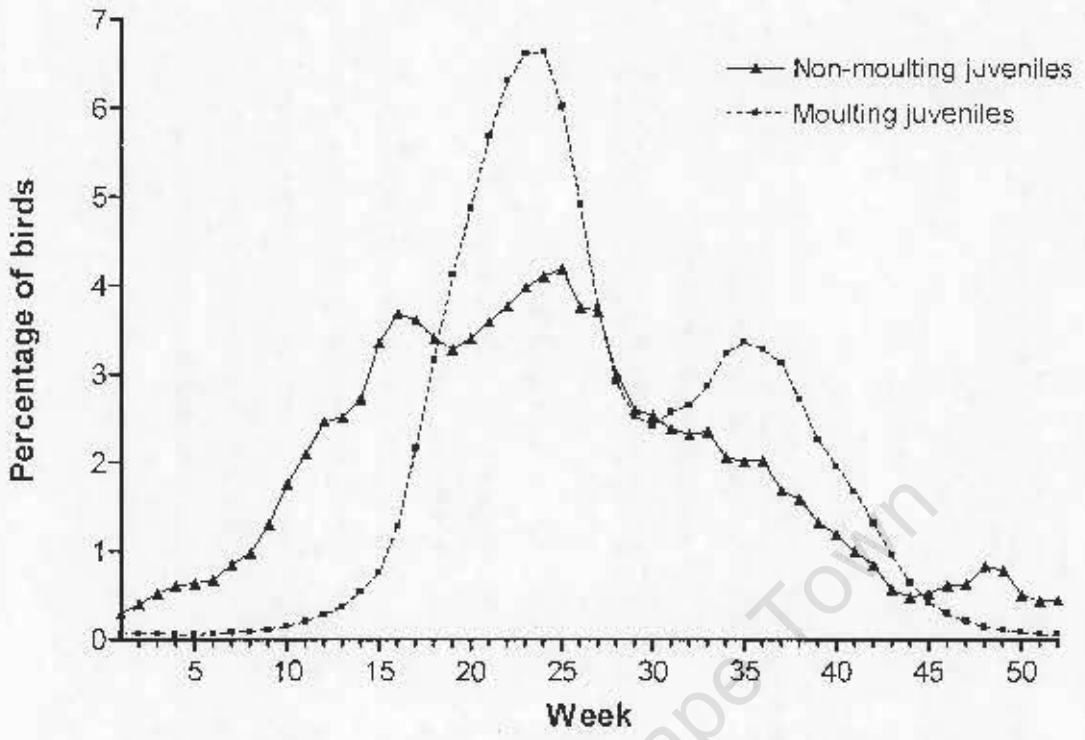

Figure 4.9 The average seasonal distribution of the number of non-moulting juvenile African Penguins present along the shoreline, compared with the average seasonal pattern of moult for juvenile penguins at Dassen Island, expressed as the percentage of birds present or moulting in each week. 1994/95-2005/06. Week 1 is the week beginning 1 July.

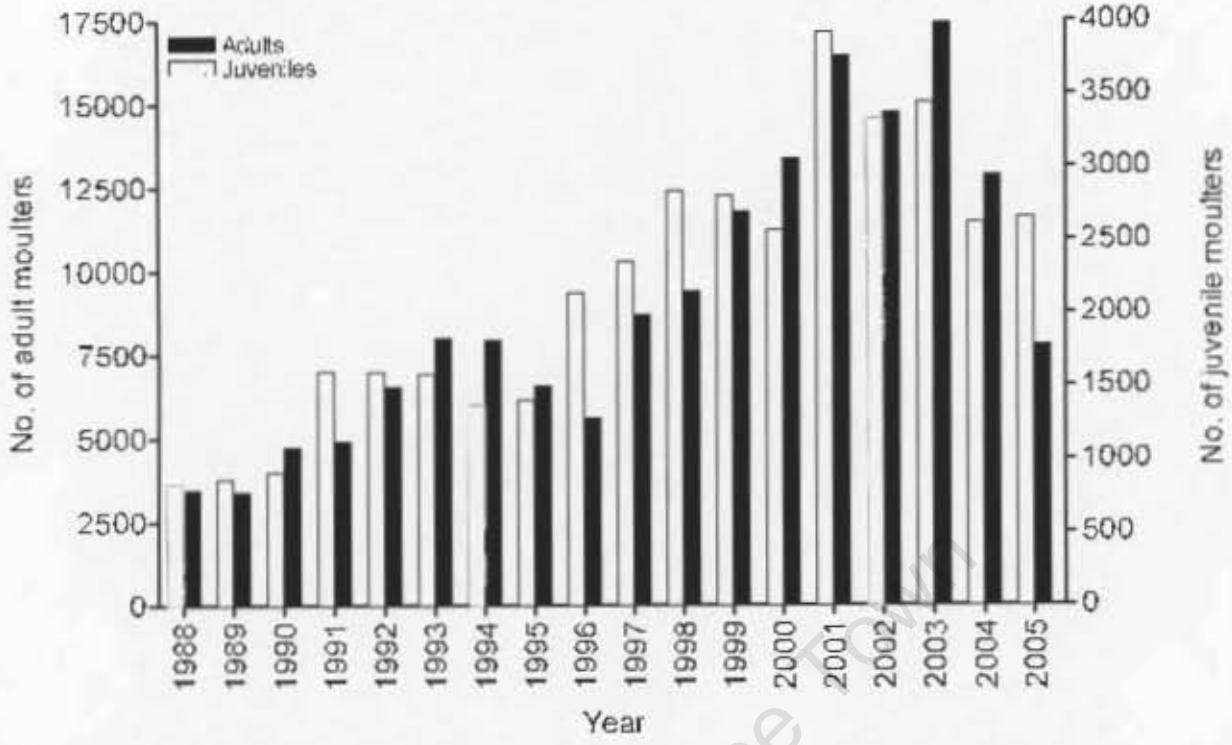

Figure 4.10 The estimated numbers of adult and juvenile African Penguins moulting per annual period (July-June) at Robben Island, 1988-2005.

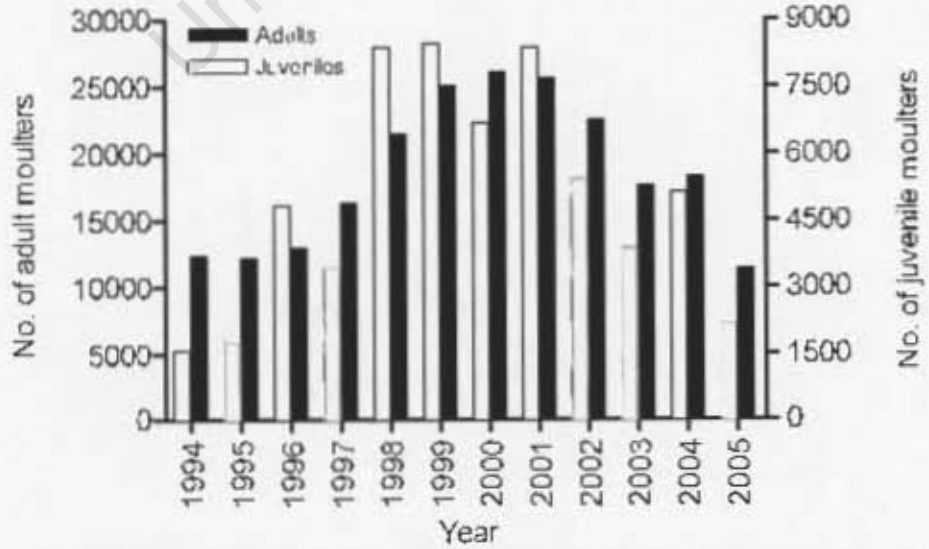

Figure 4.11 The estimated numbers of adult and juvenile African Penguins moulting per annual period (July-June) at Dassen Island, 1994-2005.

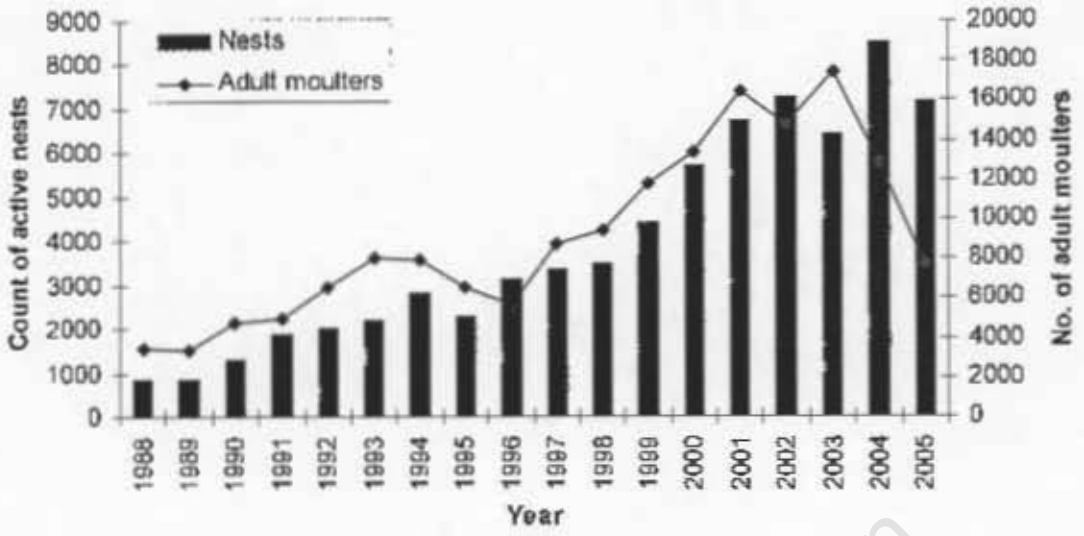

Figure 4.12 Counts of the numbers of active nest sites of African Penguins and the numbers of adults moulting during the following moult period (July–June) at Robben Island, 1988–2005.

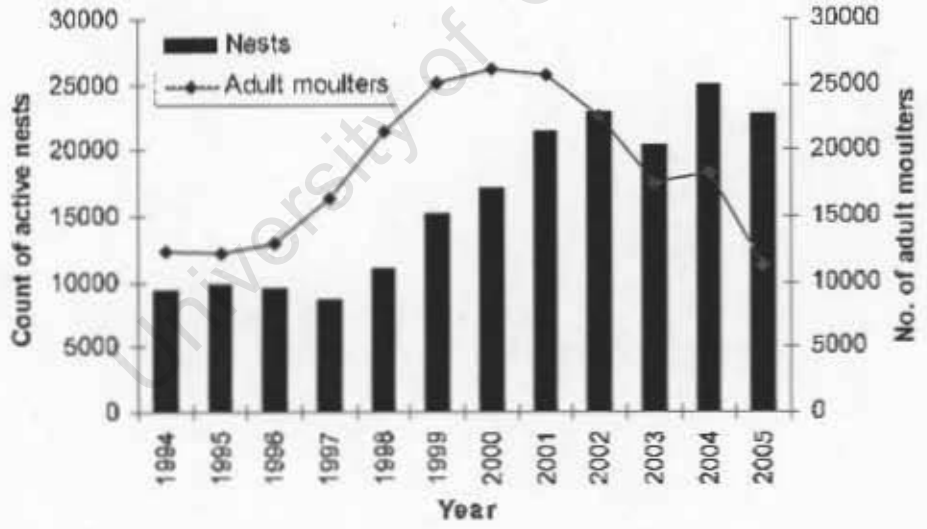

Figure 4.13 Counts of the numbers of active nest sites of African Penguins and the numbers of adults moulting during the following moult period (July–June) at Dassen Island, 1994–2005.

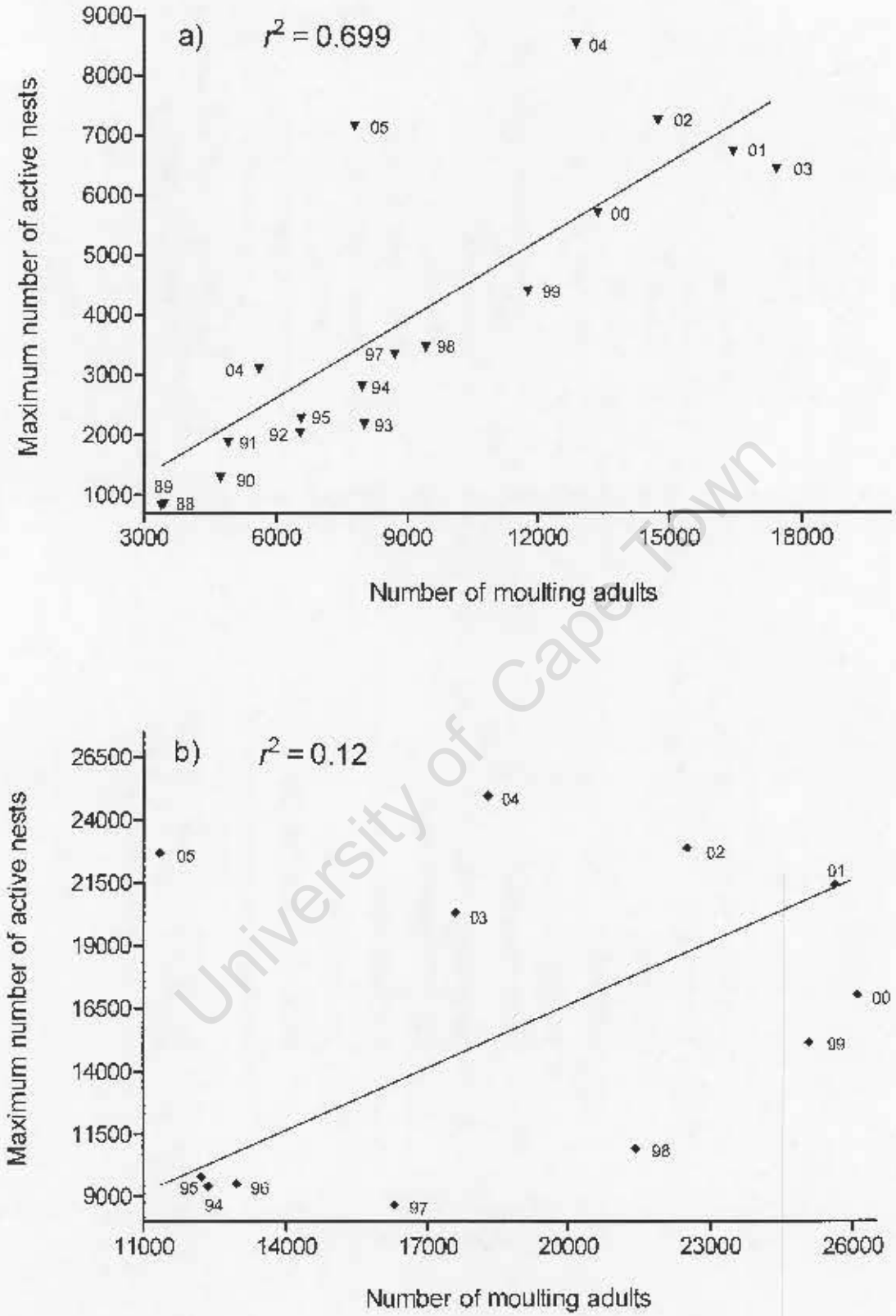

Figure 4.14 Relationships between the number of adult African Penguins moulting along the shoreline during the 12-month period July-June, and numbers of active nests preceding the peak moult of that year for a) Robben Island over the period 1988-2005 and for b) Dassen Island over the period 1994-2005. Data points are shown for each year, as well as the best-fit regression lines.

Chapter Five

Breeding success of African Penguins at Dassen Island, especially after oiling following the *Apollo Sea* spill

Breeding success of African Penguins at Dassen Island, especially after oiling following the *Apollo Sea* spill

ABSTRACT

The reproductive success of African Penguins *Spheniscus demersus* at Dassen Island from 1994 to 2000 was variable, and much larger than previously reported values for the species. Breeding success was positively related to the abundance of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax*, and the high reproductive output during the study was attributed to the large biomass and availability of these two species for much of the study period. Against this background of variable but high breeding success, de-oiled penguins from the *Apollo Sea* spill had a slightly lower hatching success than un-oiled control birds. Across the six years of the study, the overall breeding success of de-oiled birds was significantly lower than un-oiled birds, driven mainly by the reduced number of chicks which fledged. Nests with two de-oiled *Apollo Sea* parents were less successful than nests with one de-oiled bird. Chicks from nests with one de-oiled *Apollo Sea* parent grew at a similar rate to chicks from nests with no de-oiled parents. However, chicks from nests which comprised two de-oiled *Apollo Sea* birds had significantly slower growth rates than these other two groups. Breeding success and chick growth of nests with de-oiled birds were more negatively impacted when feeding conditions were less favourable. Patterns of chick mortality differed between nests with de-oiled parents and those with un-oiled birds. This difference resulted from the increased mortality of chicks 40 days and older in nests with de-oiled birds. Together with the chick growth results, this suggests that one of the main reasons for lower breeding success in de-oiled birds was their reduced ability to provision chicks, especially during the period in which the energy demands of the chicks are greatest. The rate of mate fidelity was lower in de-oiled birds than un-oiled birds, and there was a positive association between mate fidelity and breeding success.

INTRODUCTION

The *Apollo Sea* oil spill in June 1994 resulted in the contamination of approximately 10 000 African Penguins *Spheniscus demersus;* the majority (74%) of the oiled penguins were collected from Dassen Island (Dehrmann 1994). In contrast to rehabilitation efforts elsewhere (Anderson *et al.* 1996, Sharp 1996, Camphuysen *et al.* 1997, Wernham *et al.* 1997), the subsequent cleaning and treatment of the oiled penguins was successful; the post-release survival of rehabilitated birds was similar to survival rates of unaffected

birds (Underhill *et al.* 1999, 2000, Whittington 1999, 2002). Not only was the survival of rehabilitated birds from the *Apollo Sea* spill similar to that of un-oiled birds, but a substantial proportion of these rehabilitated birds was recorded breeding at Dassen Island (33°25'S, 18°05'E) (Chapter Two). The oiling did however appear to prevent breeding in some rehabilitated birds, and incurred a reproductive cost to others that did attempt breeding (Chapter Two).

Breeding success is a critical parameter influencing the population dynamics and conservation status of seabirds, including African Penguins. In oil spill events, where large numbers of individuals die, the breeding success of the restored birds (those that survive and breed after de-oiling) may be critical in contributing towards the sustainability of affected populations. Oil contamination impacts the breeding success of birds in a variety of ways. These include reduced egg productivity and hatchability (Grau *et al.* 1977, Lewis & Malecki 1984, Parnell *et al.* 1984, Harfenist *et al.* 1990, Fowler *et al.* 1995), increased nest abandonment (Butler *et al.* 1988, Eppley & Rubega 1989, 1990, Kubiak *et al.* 1989, Eppley 1992), reduced feeding rates (Burger 1997), depressed chick growth rates (Miller *et al.* 1978, Trivelpiece *et al.* 1984) and fledging weights (Giese *et al.* 2000) and reduced fledging success (Butler *et al.* 1988, Giese *et al.* 2000). Significant effects were normally dose dependent, but were often evident with even minute quantities of ingested oil. Oiling exerts a greater impact on the breeding biology of females than males for Magellanic Penguins *Spheniscus magellanicus* (Fowler *et al.* 1995) and Little Penguins *Eudyptula minor* (Giese *et al.* 2000).

African Penguins exhibit high spatial and temporal variability in breeding success. This variability is thought to be due primarily to food availability (Adams *et al.* 1992, Crawford & Dyer 1995, Crawford *et al.* 2006b). Other factors, such as the type and quality of nest (Frost *et al.* 1976, Cooper 1980, Seddon & van Heezik 1991b, Murison 1998, Kemper 2006), nest density (Siegfried 1977, Seddon & van Heezik 1991b) solitary versus colonial breeding (Cordes *et al.* 1999) and human disturbance at breeding colonies (Hockey & Hallinan 1981) are also known to influence reproductive success. Previous work on growth rates of African Penguin chicks has shown that this parameter is also highly variable, and dependent on the quantity and quality of available food (Cooper 1977a, 1980, Heath & Randall 1985, Wilson 1985). Second hatched B-chicks within a

brood generally grow more slowly than A-chicks (Williams & Cooper 1984, van Heezik & Seddon 1991).

Results from previous studies of African Penguins at Dassen Island illustrate the high variability of breeding success, with reported figures ranging from 0.37 to 0.80 fledglings per nesting attempt (Frost *et al.* 1976, Whittington *et al.* 2000). Penguins at Dassen Island breed in a range of different nest types and substrates. These include burrows excavated in sand and a shell-guano conglomerate, boulder nests, nests under shrubs (primarily *Tetragonia fruticosa*), surface nests, and nests under or within artificial structures and materials, such as shipwrecks and buildings. During the course of this study, the majority (76%) of nest types used by penguins at Dassen Island were boulder and burrow nests which are generally the most successful nest types (Cooper 1980, Seddon & van Heezik 1991b).

In this chapter, I examine the productivity of African Penguins at Dassen Island over five and a half years. I focus especially on the de-oiled *Apollo Sea* survivors, and examine breeding success and chick growth rates. Against a background of high natural variability of these parameters, I compare *Apollo Sea* birds with those that have never been oiled to determine the impact of oiling and rehabilitation on the breeding biology of African Penguins. The influence of oiling on mate fidelity rates, and the relationships between mate fidelity and reproductive success, are also investigated.

METHODS

African Penguins typically lay a clutch of two eggs, and parents share incubation and chick-rearing duties (Williams & Cooper 1984). The eggs hatch asynchronously (2–3 days apart), resulting in size asymmetries of siblings within a brood, and faster growth rates of first hatched A-chicks, compared to B-chicks (Williams & Cooper 1984, van Heezik & Seddon 1991) . Furthermore, within a brood, B-chicks are more likely to die of starvation, especially during periods of food shortage (Seddon & van Heezik 1991a, b). At Dassen Island, penguins breed throughout the year. Peaks in breeding activity occur in both winter and summer, and vary between sub-colonies on the island, and between years (Cooper 1980, Chapter Three).

A total of 18 consecutive breeding success studies was conducted between 1994 and 2000 at two study colonies (Areas G and B) on Dassen Island (Table 5.1, see Chapter Two and Figure 2.2 for locations of Areas G and B). The main aim of these studies was to compare breeding parameters of two broad study groups or nests: de-oiled *Apollo Sea* and un-oiled control penguins. At *Apollo Sea* nests, either one or both parents were de-oiled birds, and control nests contained no de-oiled birds (i.e. unaffected birds). Similar numbers of *Apollo Sea* and control nests were monitored in each study (Table 5.1). It is possible that some of the unbanded birds used as control birds may in fact have been de-oiled birds because a small percentage, estimated at below 15%, of the de-oiled *Apollo Sea* birds were released without flipper bands. However, given that the number of unbanded de-oiled birds was small relative to the total population breeding on Dassen Island, it is unlikely to have influenced the results. The majority (93%) of the birds used in control nests were unbanded. It was assumed that all unbanded birds used in the study had never been oiled because prior to the spill, apart from the small number of *Apollo Sea* birds that were not banded, the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) had banded every de-oiled penguin before it was released (South African Bird Ringing Unit (SAFRING) unpubl. data). Banded birds which formed part of the control group were confirmed to have not been de-oiled at any point by checking the records held by SANCCOB and SAFRING.

Each nest was marked with a numbered stake. Birds in study nests were sexed. Male African Penguins are generally larger than females (Hockey *et al.* 2005), with a longer and deeper culmen, although there is a small degree of overlap in measurements (Cooper 1972). The individual of the pair assessed visually as having the longest and thickest culmen was classified as the male. Nest type is known to influence breeding success in African Penguins (Frost *et al.* 1976, Cooper 1980, Seddon & van Heezik 1991b, Murison 1998, Kemper 2006), and so only burrow nests were used in this study. In both study areas (G and B), the burrows were generally excavated in a sandy substrate, rather than a shell-guano conglomerate.

In Study 1 (September 1994–March 1995), nests were checked on a daily basis; thereafter (Studies 2, 3 and 4) nests were checked three times a week. In Study 5 nests were checked on a weekly basis. From Study 6 to Study 18 nests were checked at five-

day intervals. In order to reduce failure through human disturbance (Hockey & Hallinan 1981), and to maximise the number of nests monitored at the same time (to control for the temporal variation in breeding success brought about by factors such as food availability and local weather conditions), nests were selected during incubation rather than prior to egg-laying. Once the majority of nests from one study had been followed to completion or failure, the next study commenced. There was therefore a slight degree of overlap between consecutive studies. At each nest check, the nest contents and the presence of the adult(s) were recorded. It was possible to run studies sequentially because there were breeding African Penguins at Dassen Island throughout the year.

For Studies 1–13, chicks were weighed at each nest check (intervals described above) throughout the fledging period. Chicks were weighed with Salter® spring balances, to an accuracy of 5g for chicks less than 1kg (500g spring balance), and 25g for chicks heavier than 1kg (1kg or 5kg balance). Chicks within a brood were individually marked by attaching a piece of cotton wool to the base of either the left or right flipper. The cotton wool was loosened, or replaced by a new piece, as the chick grew. Chick weight has been shown to vary more than morphometric parameters, such as flipper length and culmen length in growth rate studies of penguins (van Heezik & Davis 1990, van Heezik & Seddon 1991), and was therefore the only parameter measured in this study. Weight was considered sufficient to detect any differences in the quality of chicks produced by *Apollo Sea* parents compared to those of un-oiled birds. In Studies 14–18 nests were checked at five-day intervals, but chicks were not weighed.

Eggs were considered to be infertile if they survived to the hatching period, but did not hatch. If one egg within a clutch hatched and the other did not, the egg that did not hatch was assumed to be infertile. If a clutch of two eggs was incubated beyond the maximum recorded incubation period of 41 days (Hockey *et al.* 2005) and neither of the eggs hatched, these were also considered to be infertile. Chicks were deemed to have fledged if they had left the nest and could not be found in the colony after reaching a mass of 2kg or greater, and were fully feathered.

Breeding success was assessed in two ways: 1) incubation success, which included clutch size (or apparent clutch size because nests were not monitored from egg-laying) and hatching success (proportion of chicks hatched from eggs laid, and per nest);

2) fledging success (the proportion of chicks fledged from the number of chicks hatched, and per nest). The incidence of infertile eggs and the incidence of second and replacement clutches were also investigated. Second clutches were those laid after a successful breeding attempt, and replacement clutches followed a failed breeding attempt. Because individual nests were not monitored throughout the study period, it was not possible to assess the breeding frequency and incidence of second and replacement clutches directly. It was also not known whether breeding attempts monitored represented initial, replacement or second clutches. However, the re-sighting database was used to determine the breeding interval following successful and failed breeding attempts for all banded birds used in breeding studies. Given the potential for brood reduction in African Penguins (Randall 1983, Williams & Cooper 1984, but see Seddon & van Heezik 1991a, b, Seddon 1999), the proportion of nests fledging two chicks and the proportion of partial failures/successes and complete failures were also assessed. I also investigated the pattern of chick mortality in the different study groups by classifying penguin chicks that died into one of three age categories: < 5 days, 6–40 days and > 40 days.

To reduce the potential bias resulting from not having monitored study nests from the beginning of the breeding attempt (egg-laying), the Underhill (submitted) extension of the Mayfield (1961, 1975) method of calculating nest success was used. A generalized linear model was used to determine the probability of survival through the incubation and fledging periods, and to examine the effects of explanatory variables on the breeding success of penguins at Dassen Island. For these analyses, the incubation period was defined as 40 days (Rand 1960, Williams & Cooper 1984, Randall 1989), and the fledging period as 74 days, the median fledging period for successful nests in this study. For models that included egg-laying date as an explanatory variable, this was back-calculated from the hatching date; for those nests that failed before hatching, the egg-laying date was estimated by subtracting the number of incubation days that the nest survived (and was monitored) from the mean incubation period (40 days), dividing by two, and subtracting this figure (in days) from the date the nest was first found with eggs. Successful nests were those where one or two eggs hatched (for incubation success) and one or two chicks fledged (for fledging success). Partial losses were therefore ignored. I modelled the logarithm of the parameter λ of an exponential distribution as a linear combination of the explanatory variables (see Underhill submitted for details). For

example, for three explanatory variables $\log \lambda = a + b_1x_1 + b_2x_2 + b_3x_3$. The models were fitted using the RSURVIVAL procedure in GenStat 8 (GenStat Committee 2005). For a variable to be included in the model, it needed to be statistically significant in terms of model selection procedures that incorporate the percentage of deviance explained (Dobson 2002), and it needed to reduce the value of the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). In this way the model that optimally balances the goodness of fit and the number of parameters is selected. The explanatory variables tested in the models for both incubation and fledging success are listed and explained in Table 5.2.

Chick growth analysis

The growth rates of penguin chicks were analysed using the non-parametric statistical approach developed by le Roux & Underhill (in prep.).This was preferred to fitting a parametric model over the entire growth period, which may be a poor approximation of the actual growth, and may also present analytical problems (Brisbin *et al.* 1987, Gochfeld 1987, Zach 1988). Growth rates were calculated between each pair of successive measurements. So, if successive masses at times t and u were m_t and m_u, the growth rate over this time period is g = (change in size)/(time period) = $(m_t–m_u)/(t–u)$ and the mean of the pair of measurements is $a = (m_t+m_u)/2$. All the pairs of values (a, g) were plotted, resulting in a growth-rate against mass plot.

For a set of target masses at small increments between hatching mass and fledging mass, the average growth rate at each of these masses was estimated using weighted regression. Full details of the algorithm are contained in le Roux & Underhill (in prep.); the method is described briefly here. For the target mass at which the growth rate was estimated, weights for all pairs of observations were calculated (a, g) in such a way that values close to the target mass had large weights and values farther away had increasingly smaller weights. If the target mass was m^*, then the weight w attached to observation (a, g) was $w = \exp(-((a-m^*)/\sigma)^2)$ where σ was chosen to be 200. This is about 6.5% of the adult mass. This results in weights attached to observations 200g distant from the target mass being substantial (weight 0.37), at 300g from the target mass the weight (0.105) is small, and at 400g distant the weight (0.018) is tiny. Observations more than 400g distant from the target mass thus contribute negligible weights to the regression calculations. A weighted linear regression was fitted to predict

growth rate from mass using these weights. The regression line, fitted by GenStat8 (GenStat Committee 2005), was used to predict the growth rate g^* at the target mass. Using this weighted approach, the estimated growth rate depends on observed growth rates in the neighbourhood of the target mass. By varying σ, the extent of the influential neighbourhood can be modified. The value for σ (200) was selected by visual inspection. However, the results do not depend critically on the choice of a particular value for σ. Experimentation showed that if a chosen value was twice as large or half as small, the results would have been nearly identical.

An approximate standard deviation of mass was estimated for each target mass. The same weights used for the regression were used to estimate a weighted standard deviation s_{m^*}; the formula $s_{m^*} = (1/\sum w)((w(g-g^*)^2)$ was used. An approximate coefficient of variation for each target mass was calculated as $CV^* = 100 \times (s_{m^*}/m^*)$. This coefficient of variation provides a measure of the variability of the growth rate for each target mass.

The estimated growth rates at each target mass were plotted, and the points were linked by interpolation. Likewise, approximate lower and upper confidence limits for the growth rates were plotted. A normal distribution was assumed, so that the lower and upper confidence limits were $g^*-1.96\ s_{m^*}$ and $g^* + 1.96\ s_{m^*}$ respectively. Using hatching mass as the starting value on day 0, the growth rate curve was integrated to produce a plot of mass against time. This provides a non-parametric growth curve which describes the pattern of growth as determined by the data rather than forcing the data into a pattern as a consequence of the parametric model chosen by the analyst.

For each successive pair of measurements of a chick, a comparison was made between the observed growth rate and the expected growth rate in the interval between the two measurements. The expected growth rate was computed as the average of the two measurements, and its approximate standard deviation calculated as described above. The standardized growth rate was then computed using the conventional approach to standardization – dividing the difference between the observed and expected growth rate by the standard deviation. In symbols, if the observed growth rate is g, the predicted growth rate is g^* and the estimated standard deviation at this growth rate is s^*, then the standardized growth rate z is defined to be $z = (g-g^*)/s^*$. For large samples, the overall mean of all z-values is asymptotically zero; negative values indicate below average

growth rates and positive values indicate above average growth rates. The z-values can be interpreted as an index of the extent to which growth in the interval is above or below expected; through the mechanism of dividing by the standard deviation, the index is independent of the stage of growth. In other words, the z-values, which are dimensionless, represent a common currency to measure departures from "average" growth, which are independent of whether growth is measured early when the absolute growth rates (g/day or mm/day) tend to be small, at the maximum growth spurt, when growth rates tend to be large, or late in growth, when growth rates tend to be decreasing.

If the scores are assumed to be normally distributed (which to a first approximation is probably reasonable), the magnitudes of z-values can be expected to be in keeping with the standard normal distribution; for example, approximately 95% of the z-values can be anticipated to lie between the values –1.96 and +1.96; less than 0.5% of the values can be anticipated to be smaller than –2.58 or larger than +2.58. All z-values above or below +2.58 and –2.58 respectively were screened for possible erroneous measurements or entries.

Because the index is independent of growth stage, it becomes possible to investigate the effect of explanatory variables on growth rates. In each study I compared z-values of chicks from five study groups: 1) all nests, 2) control nests (no de-oiled parents), 3) nests with an *Apollo Sea* male, 4) nests with an *Apollo Sea* female and 5) nests with an *Apollo Sea* pair. I also relate the standardized growth rate per chick to a range of explanatory variables using multiple regression analysis. The explanatory variables tested include Study (Study 1–13), Area (G or B), Success/Failure (whether a chick successfully fledged), Brood Type (singleton, A- or B-chick) and Study group (Rehabilitation code). For Brood Type, singletons are chicks from a one chick brood; A- and B-chicks are respectively the first and second hatched chicks from a two chick brood. I also tested whether there were any interactions between these variables. As with the generalized linear models used for the breeding success analyses, only variables that were found to have a significant effect on chick growth rate (z-values) were ultimately incorporated into the model.

The relationship between the availability of food and breeding success was investigated using correlation analysis. Estimates of the biomass of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax*, the main prey items of African Penguins in the Western Cape in recent years (Berruti *et al.* 1989, Crawford & Dyer 1995, Crawford *et al.* 2006b) were obtained from Marine and Coastal Management.

The fidelity of de-oiled *Apollo Sea* birds to their mates was quantified, and compared with control birds (those that were flipper-banded), by measuring three parameters for both groups of birds: 1) re-unite rate (the rate at which birds observed breeding together paired again with the same partner in the subsequent breeding attempt), 2) divorce rate (rate at which birds paired with a different partner in the subsequent breeding attempt even though its previous partner was known to be alive) and 3) widow rate (the proportion of birds which changed partners in subsequent breeding attempts, where the previous partner was considered to be dead). The death of partners was based on the actual recoveries of dead birds or due to the absence (based on re-sighting data) of the previous partner from the date of the subsequent breeding attempt onwards.

These parameters were calculated as defined by the late Mike Cullen and Phillip Island Nature Park (unpubl. data):

Re-unite rate = R/(R+D)*100%
Divorce rate = D/(R+D)*100%
Widow rate = W/(R+D+W)*100%

where R was the number of times birds re-united, D was the number of times that birds changed partners as a result of a divorce, and W was the number of times that birds changed partners as a result of their partner having died.

The analyses were restricted to birds included in the breeding success studies. Pair bonds were defined as any pairing of birds which resulted in eggs or chicks. Re-sightings of pairs prospecting or courting at a nest site were, therefore, not included. Only pairs in which both partners were flipper-banded were included in the analyses. The control group comprised birds that had been flipper-banded previously for other studies (none had ever been oiled).

I investigated whether prior reproductive success influenced mate fidelity by determining whether there was a tendency for birds to re-unite more frequently if they successfully raised a chick in the previous breeding attempt. For each bird, I recorded whether it was an *Apollo Sea* or control bird, and whether it had successfully raised at least one chick in the previous breeding attempt. These were used as explanatory variables in a logistic regression with a binomial distribution and a logit link function, the response variable being whether the bird re-united (response = 1) or not (response = 0). I also used a logistic regression model to investigate whether birds that re-united were more successful at rearing chicks than those that divorced their previous partner. Whether the bird had re-united with or divorced its previous mate, and its rehabilitation status (*Apollo Sea* or control) were used as explanatory variables; the response variable was whether the bird successfully raised at least one chick (response = 1) or not (response = 0).

RESULTS

Breeding success

Between 1994 and 2000, a total of 1 465 nests was successfully monitored over 18 consecutive studies. These comprised 767 *Apollo Sea* nests and 698 control nests. The breeding success parameters for the different study groups are summarised in Table 5.3. Most nests (95%) had two-egg clutches. The proportion of one-egg and two-egg clutches was similar for *Apollo Sea* and control nests (Fisher's exact test, $P = 0.27$). There was also no significant difference in the proportion of one and two egg clutches between nests with *Apollo Sea* females and those with control birds (Fisher's exact test, $P = 0.21$). The mean apparent clutch size (not accounting for eggs that may have been lost prior to the nest being monitored) for all nests across the 18 studies was 1.94 (SD = 0.24, $n = 1465$ nests). The mean clutch sizes for *Apollo Sea* nests, 1.93 (SD = 0.26, $n = 767$), and control nests, 1.95 (SD = 0.23, $n = 698$), were similar ($t = 1.178$, df = 1463, $P = 0.24$; Table 5.3). A minimum of 10.9% of eggs from *Apollo Sea* nests were infertile. This figure does not include eggs that were deserted before the end of the incubation period. Although the proportion of infertile eggs was higher than that of eggs in control nests (9.2%), the difference was not statistically significant (Fisher's exact test, $P = 0.09$; Figure 5.1).

Across the six years of the study, the mean number of hatchlings produced per nest was 1.31 (SD = 0.45, n = 767) in *Apollo Sea* nests, 6% lower than the 1.39 (SD = 0.45, n = 698) for control nests; however this difference was not formally statistically significant (t =1.948, df = 1463, P = 0.052). The proportion of chicks hatched from the number of eggs found was 67.8% for *Apollo Sea* nests and 71.7% for control nests (Table 5.3). The mean number of chicks fledged per nest varied between 0.35 (SD = 0.62, n =79) in Study 2 and 1.30 (SD = 0.81, n = 83) in Study 13 (Figure 5.2). The overall mean for all nests over the 18 studies was 0.89 (SD = 0.87, n = 1465; Table 5.3). The mean number of chicks fledged per nest was correlated with the mean number of chicks hatched per nest (r_s = 0.765, df = 16, P < 0.001). Overall, *Apollo Sea* nests fledged 11% fewer chicks per pair than control nests (t = 2.437, df = 1463, P = 0.015). The reduced productivity of *Apollo Sea* nests was most noticeable in studies in which the productivity of all nests was relatively low, such as in Study 2 and Study 7. In these studies the productivity of all nests was markedly lower than the average breeding success for the entire study, the reduction being greatest for *Apollo Sea* nests (Figure 5.2). Expressed as a proportion of the total number of chicks hatched, fledging success was 63.7% for *Apollo Sea* nests and 67.8% for control nests. Of the nests where eggs hatched, the proportion that fledged two chicks, experienced partial losses/successes and complete failures differed between study groups (X^2 = 16.6, df = 8, P = 0.034; Table 5.4). *Apollo Sea* nests fledged two chicks less frequently than control nests (Fisher's exact test, P = 0.038, Table 5.4). Nests with two *Apollo Sea* adults (i.e. *Apollo Sea* pairs) fledged two chicks even less frequently (37.3% compared to 39.4% for *Apollo Sea* nests, and 48% for control nests), and also had a greater proportion of complete losses, where no chicks fledged from eggs that hatched (Table 5.4).

Influence of food availability

The mean number of chicks fledged per pair (per breeding attempt) was variable, but generally increased during the course of the study (Figures 5.2 & 5.3). When studies were combined for each calendar year from 1995 to 1999, the mean number of chicks fledged per breeding attempt was positively related to the spawner biomass of Sardine and Anchovy (r = 0.887, df = 3, P = 0.022 and r = 0.842, df = 3, P = 0.036, respectively; one-tailed tests). Similarly, over the five year period the combined spawner biomass of

Sardine and Anchovy explained 78% of the observed variation in breeding success ($r = 0.886$, df = 3, $P = 0.023$, Figure 5.3).

Patterns of chick mortality and fledging period

Chick mortality was generally highest soon after hatching and declined with age (Figure 5.4). The pattern of chick mortality differed between the study groups (Figure 5.4, Table 5.5). Of chicks that died, 31% of those from control nests died within five days of hatching; for all *Apollo Sea* nests and those with two *Apollo Sea* adults, the percentage that died within five days of hatching was 25% and 9% respectively (Table 5.5). Twenty-three percent of chick mortalities in the *Apollo Sea* nests (and 26% for nests with *Apollo Sea* pairs) occurred when chicks were older than 40 days, compared with 12% for control nests. The difference in chick mortality rates between the *Apollo Sea* and control nests was significant ($X^2 = 13.4$, df = 2, $P = 0.0012$) and that between *Apollo Sea* pairs and control nests highly significant ($X^2 = 22.0$, df = 2, $P < 0.001$).

For chicks that fledged, the fledging period ranged from 40 days to 119 days. The median fledging period for all nests was 74 days ($n = 815$). The lower part of the range for fledging period is likely to be an underestimate. For studies in which nests were checked at intervals of five days (Studies 6 – 18) and seven days (Study 5), the error associated with the calculation of fledging periods could be up to eight and 12 days respectively. This includes the intervals between hatching and the first nest check thereafter, and fledging (the disappearance of a fully feathered chick) and the following nest check. It is likely that that some of the chicks that fledged, especially those that "fledged" at young ages (less than 60 days) may have wandered from their nest (thereby evading detection) towards the end of the fledging period, thus underestimating the actual fledging period for these birds. When chicks disappeared from their nest, neighbouring nests and crèches were checked for the presence of the "missing" birds. Chicks were only considered to have fledged if they were fully feathered and weighed more than 2kg at the last nest check, so even if chicks were present at the colony for some time after they were last detected, it is unlikely that they would have died after the last nest check. Furthermore, chicks that died after a prolonged period of mass loss were normally found dead in the colony. The mean fledging period for all nests differed between studies, ranging from 65.8 days (SD = 11.0, $n = 69$) in Study 6 to 82.7 days (SD = 10.7, $n = 28$) in Study 2. The mean fledging period was significantly related to the

mean number of chicks fledged per pair (r_s = –0.557; P = 0.016); longer fledging periods were associated with lower breeding success. The mean fledging periods were similar for *Apollo Sea* and control nests (Table 5.3).

Breeding frequency and the incidence of second and replacement clutches

Of the nests which were monitored during the study period, 56% (n = 815) successfully fledged a chick. Twenty-four percent (n = 348) of the nests failed during incubation, and 20% (n = 302) failed at the brood stage. Re-sightings of study birds after the completion, or failure, of a monitored breeding attempt provide an indication of the incidence of replacement and second clutches. For pairs which successfully fledged a chick and which were subsequently re-sighted breeding, the median interval between the chick(s) fledging and re-laying was 4.7 months, with no difference between *Apollo Sea* and control nests (Mann-Whitney U = 17 710, n_1 = 357, n_2 = 101, P = 0.79). Twenty-five percent of these pairs re-laid within 2.5 months of successfully fledging a chick (Figure 5.5). The interval varied from five days to 57 months. In the case of the former, S20774, a female *Apollo Sea* bird, and A5647, an un-oiled male in Study 16, successfully fledged one chick around 7 May 1999 (the last date on which the chick was recorded at the nest). The chick was weighed on the last few nest checks and had been gradually losing weight from 26 April, when it weighed 2 500g, until fledging 11 days later when it weighed 2 250g. Loss of weight towards the end of the fledging period is not unusual for African Penguin chicks (Williams & Cooper 1984, van Heezik & Seddon 1991), and suggests that the parents may have "abandoned" the chick before it eventually left the nest. On 12 May 1999 (five days later), S20774 was re-sighted in the same nest with one fresh egg; by 17 May a second egg had been laid. This breeding attempt was monitored as an *Apollo Sea* study nest in Study 17. In this breeding attempt, the pair successfully fledged two chicks by the end of August 1999. The median interval between a successful breeding attempt and the laying of a second clutch was shortest for birds in Study 16 (median interval = 51.5 days, n = 50 nests). Breeding success in Study 16 and Study 17, which followed, was higher than the average for the entire study, but were not the highest recorded during the study period (Figure 5.2).

For nests which failed, the median interval between the failed attempt and re-laying was 4.4 months (n = 160) for nests that failed at the incubation stage and 5.3 months (n = 135) for nests that failed at the brood stage. Thirty-six percent of the pairs that failed

at the incubation stage re-laid within 2.5 months; for pairs that failed at the brood stage, this proportion was 21% (Figure 5.5). There were no significant differences between the *Apollo Sea* and control nests in either the median interval between egg failure and re-laying (Mann-Whitney $U = 880$, $n_1 = 147$, $n_2 = 13$, $P = 0.64$) or between chick failure and re-laying (Mann-Whitney $U = 779$, $n_1 = 122$, $n_2 = 13$, $P = 0.92$).

Factors affecting breeding success

The probability of a nest surviving the incubation period (incubation success, defined as nests where at least one egg hatched), was modelled using the explanatory variables in Table 5.2. The only significant explanatory variable was "Study" indicating that there was variability in incubation success between the 18 studies, but that there was no significant difference in incubation success between *Apollo Sea* and control nests (Table 5.6). For fledging success (the probability that a nest fledges at least one chick) the model which best explained the data included "Study", "Area" and "Rehab2" as the explanatory variables (Table 5.7). The model suggests that there was variability in fledging success between studies; nests in Area B had a lower probability of fledging a chick, and nests with two *Apollo Sea* parents (*Apollo Sea* pairs) had a lower probability of fledging a chick than any of the other nests (those with an *Apollo Sea* female or male, or control nests), with no significant difference between nests with only one *Apollo Sea* parent and control nests (Table 5.7). Interaction between variables did not improve the fit of the model. Inserting time variables did not improve the fit, indicating there was no change through time of the *Apollo Sea* pair effect.

The modelled value of the parameter λ for a nest in a particular study is computed from the regression coefficients of Table 5.7. For example, the modelled value of λ for a nest from Area G in Study 4 is given by:

$$\log_e \lambda = -5.779 - 0.084$$

where –5.779 is the constant and –0.084 is the regression coefficient for Study 4. Thus $\log_e \lambda = -5.863$ and $\lambda = 0.002843$. For the exponential distribution, the probability that a nest survives the fledging period is given by:

$$\Pr(\text{breeding attempt fails after } p \text{ days}) = \int_p^{\infty} \lambda e^{-\lambda x} dx = e^{-\lambda p},$$

where, in this case, p = 74 days from hatching to fledging, so that the probability of success is 0.81.

For a nest with an *Apollo Sea* pair from Area G in Study 4,

$$\log_e \lambda = -5.779 - 0.084 + 0.469$$

where the additional regression coefficient for the *Apollo Sea* pair variable (0.469) is included and λ = 0.004544; the probability that a breeding attempt is successful is 0.71. This equates to a reduction in fledging success of about 10% for *Apollo Sea* birds. If the coefficient for Area B is included, then

$$\log_e \lambda = -5.779 - 0.084 + 0.469 + 0.383$$

and λ = 0.006664; the probability of at least one chick being fledged from nests where chicks hatched is 0.61, which is 12% less than the probability of success for all other nests from Area B in Study 4, and 20% less than other nests from Area G.

These values represent the modelled probabilities of different groups of nests in Study 4 being successful in raising at least one chick beyond the median fledging period. The extent of the differences between *Apollo Sea* and other nests and between Area G and Area B ranged from 5% to 17% and 4% to15% respectively; the differences tended to be greater in studies with lower overall fledging success (Table 5.8).

Chick growth rates

A total of 955 chicks were weighed on more than one occasion (from hatching until failure or fledging – see Methods for details of intervals for the different studies) during the course of this study. In Study 1, the only study in which nests were checked daily, the mean mass of chicks within one day of hatching was 98 g (SD = 11g, n = 29) for control nests and 100 g (SD = 12 g, n = 46) for *Apollo Sea* nests. The difference between the groups was not significant (t = 0.936, df = 73, P = 0.35). The growth rate from c. 400 g to 1 160 g was fairly constant at about 45g per day, decreasing gradually thereafter (Figure 5.6a). The peak growth rate occurred at 960g, when the growth rate

was 46.7g/day. The mass at the median fledging age (74 days) was 2 640g (Figure 5.6b). At this mass the mean growth rate was 21.5g/day. The mean mass increased to 2 960g by 90 days after hatching (Figure 5.6b). The rate of growth showed a large degree of variation (Figure 5.6a). This variation in growth rates increased with the age of the chick. For example, at 2 760g (80 days after hatching), the mean growth rate was 19.7g/day (SD = 32.78, n = 386), with an approximate 95% confidence interval from –44.6g/day to 83.91 g/day. The transformation of the growth rate against mass plot into a growth rate curve showing mean mass in relation to age indicates nearly linear growth in mass from 10 to 40 days after hatching (Figure 5.6b).

The z-values, which measure the extent to which a chick is growing slower or faster than the expected growth rate for its size (baseline), varied between studies, and between study groups (Figure 5.7). In studies where all of the groups performed relatively poorly (such as in studies 2 and 7), chicks from nests with *Apollo Sea* pairs had noticeably slower growth rates than the other study groups (Figure 5.7). The one exception to this pattern was in Study 5, where most of the study groups had z-values close to or above the baseline; the nests with *Apollo Sea* females performed slightly below average, and nests with *Apollo Sea* pairs performed even worse (Figure 5.7). From Study 8 onwards, the z-values were generally similar or better than the baseline for all study groups, indicating that improved breeding success during this period (Figures 5.2 & 5.3) was accompanied by improved growth rates of chicks. There was also within-study variation in the growth rates of chicks; average z-values per five day period deviated above and below the baseline throughout the study period, without any clear seasonal or annual pattern (Figure 5.8).

The estimates and results of the multiple regression model of the average z-value per chick (response variable) on a range of explanatory variables are provided in Table 5.9. The regression coefficients from Table 5.9 are used to compute the modelled value of z. So, for a particular chick, z is computed as:

> z = – 0.218 (constant) + (coefficient for Study No.) + 0.146 (if Area = G) – 0.235 (if chick did not fledge) – 0.050 (if study group = *Apollo Sea* pair) + (coefficient for brood type) + (coefficient for interaction term, see Table 5.10).

For example, the z-value of an A-chick that fledged from a reference study group nest (control nests and nests with one *Apollo Sea* parent) from Area G in Study 2 is:

$$z = -0.0218 - 0.201 + 0.146 + 0.004 = -0.0728$$

For B-chicks that failed from a nest with an *Apollo Sea* pair in Area G, in the same study, the z-value would be:

$$z = -0.0218 - 0.201 + 0.146 - 0.235 - 0.051 - 0.107 - 0.375 = -0.845$$

Growth rates of chicks were significantly reduced in Study 2, and were significantly faster in Study 6 and Studies 10–13, compared to the reference study (Study 1) (Table 5.9; see also Figures 5.7 & 5.8). Overall, growth rates of chicks from nests in Area G were higher than those in Area B. Growth rates of chicks that fledged were greater than chicks that did not fledge. Successful singletons grew at a similar rate to successful A-chicks within a two chick brood ($t = 0.07$, df = 931, $P = 0.946$, Table 5.9); B-chicks that fledged grew at a significantly slower rate than successful singletons ($t = -2.03$, df = 931, $P = 0.043$) and A-chicks. The interaction between brood type and the variable which indicates whether a chick fledged or failed was significant (Tables 5.9 & 5.10), indicating that, for chicks that failed both A- and B-chicks grew slower than singletons, this difference being much larger for B-chicks (Table 5.10). The growth rates of chicks from nests with one *Apollo Sea* parent, either male or female, was similar to chicks from control nests (with no de-oiled parents). However, chicks from nests with a pair of *Apollo Sea* parents had significantly slower growth rates than all other study groups ($t = -1.65$, df = 931, $P = 0.045$, Table 5.9). The model accounted for 37% of the variation in growth rates of chicks.

Mate fidelity

Between 1995 and 2000, 60 of the 122 de-oiled *Apollo Sea* birds for which information was available had only one mate. Of the 62 birds which changed partners during the course of the study, 53 were recorded with two mates, eight with three mates and one bird was recorded breeding with four different birds. In total 33 of the 41 un-oiled control birds retained the same mate throughout the study. The remaining eight birds each had two mates. During the course of this study de-oiled *Apollo Sea* birds were recorded with

a mean of 1.59 mates (SD = 0.65, n = 122 birds), significantly greater than the 1.19 mates (SD = 0.40, n = 41 birds) recorded for un-oiled control birds (t = 3.68, df = 161, P < 0.001). The rate at which de-oiled *Apollo Sea* birds re-united with their previous mate was 64.8%, compared with 87.5% for control birds (Table 5.11). The lower re-unite rate of *Apollo Sea* birds was almost entirely due to a significantly greater divorce rate in *Apollo Sea* birds (35.3%) than for control birds (12.5%) (X^2 = 8.7, df = 2, P = 0.013, Table 5.11), although the widow rate of *Apollo Sea* birds was also greater than that of control birds. The was no difference in the re-unite, divorce and widow rates between *Apollo Sea* males and females (X^2 = 1.2, df = 2, P = 0.56), or between control males and females (X^2 = 4.9, df = 2, P = 0.09).

For the 215 penguins for which data were available, the generalized linear model (linear regression) for the probability p of re-uniting, for all birds, was

$$\text{(logit) } p = \frac{e^y}{1+e^y} \text{ where } y = 0.101 + 1.529S \text{ (for all birds)}$$

The outcome of the previous breeding attempt (S) was 1 if the bird (and pair) successfully raised at least one chick to fledging and 0 if no chicks were successfully reared.

For *Apollo Sea* birds the probability of re-uniting was

$$\text{(logit) } p = \frac{e^y}{1+e^y} \text{ where } y = 0.135 + 1.328S - 1.053A$$

where A represented the rehabilitation status of the bird (1 for *Apollo Sea* birds and 0 for control birds).

The positive coefficient of S indicated that the probability of a bird re-uniting with its previous mate was greater if they had bred successfully during the prior attempt (P < 0.001). For all birds, the probability of re-uniting was 0.525 following a failed breeding attempt, and 0.836 following a successful attempt (Table 5.12). The negative co-efficient

of *A* indicated that, after the influence of breeding success had been accounted for, *Apollo Sea* birds were less likely than control birds to re-unite with their mates (Table 5.12).

The fitted model for the probability *p* of successfully rearing at least one chick to independence, was

$$\text{(logit) } p = \frac{e^{y}}{1+e^{y}} \text{ where } y = 0.061 + 0.809R \text{ (for all birds)}$$

where *R* was 1 if birds re-united with their previous mate and 0 if they divorced their previous mate and bred with a new partner.

For *Apollo Sea* birds, the probability of successfully rearing a chick was

$$\text{(logit) } p = \frac{e^{y}}{1+e^{y}} \text{ where } y = 0.711 + 0.714R - 0.680A$$

On the basis of the positive co-efficient of *R*, penguins that re-united with their mates had a greater probability of raising a chick than birds that paired with new mates ($P = 0.008$). Overall, the probability of successfully rearing a chick was 0.515 for birds that divorced and re-mated, and 0.705 for birds that re-united with their mates from the prior breeding attempt (Table 5.13). The negative co-efficient of *A* indicated that, even after accounting for the influence of mate retention and divorce, *Apollo Sea* birds had a lower probability of a successfully rearing a chick, when compared with control birds (Table 5.13).

DISCUSSION

Breeding success and influence of food availability

Variability in reproductive output is a common feature of seabird demography, and is influenced by a complexity of factors. Ashmole (1971) identified food availability as one of the key factors influencing breeding success in seabirds. Even within a species, there

can be significant spatial variation in breeding success (e.g. Fortescue 1999, Kemper 2006). Marked interannual variation in breeding performance is a characteristic feature of African Penguin breeding biology (Randall 1983, Wilson 1985, La Cock *et al.* 1987, Crawford *et al.* 1999, 2006b), and food availability is known to be an important determinant of breeding success (Adams *et al.* 1992, Crawford & Dyer 1995, Crawford *et al.* 2006b). The significant relationships obtained between fledging success and the combined spawner biomass of Anchovy and Sardine confirm the important influence of food on breeding success for African Penguins. This relationship is further supported by the negative correlation between breeding success and fledging period, which suggests that in studies with lower breeding success the birds were finding it more difficult to obtain food and therefore taking longer to fledge chicks. The abundance of food accounted for 78% of the variation in breeding success. During the last few years of the study (1997–1999), a substantial increase in the abundance of Anchovy and Sardine (Barange *et al.* 1999), are thought to have contributed towards improved recruitment of penguins to the breeding populations at Dassen and Robben (33°48'S, 18°23'E) Islands (Wolfaardt *et al.* 2001), and to significantly increased breeding success at Robben Island (Crawford *et al.* 2006b).

Reproductive success of African Penguins at Dassen Island during this study was variable, but comparatively high in relation to previous studies. Indeed, the mean number of chicks fledged per pair per breeding attempt (0.89) is the largest reported for the species (see Hockey *et al.* 2005 for a summary of previous results). This figure represents the number of chicks fledged per breeding attempt over the six-year period of the study. The mean number of chicks fledged per year would therefore be even larger if double-brooding were taken into account. Because penguins frequently re-lay at a considerable distance from their first nests, it was not feasible to measure double brooding directly. However, the re-sightings of banded penguins that formed part of breeding studies indicate that African Penguins at Dassen Island had a sub-annual breeding cycle. Furthermore, the time elapsed between breeding attempts suggests that a relatively high percentage of birds re-laid after both successful and failed breeding attempts than has previously been reported for African Penguins from west coast colonies.

In species such as the African Penguin which are not strictly seasonal breeders (Chapter Three), but rather have an extended breeding season, it is difficult to quantify the incidence of second clutches and replacement clutches. In this study, 25% of banded birds that were observed breeding after a monitored breeding attempt, bred again within 2.5 months of successfully fledging a chick. For birds that failed at the incubation and brood stages, the proportions that re-laid within 2.5 months were 36% and 21%, respectively.

These results are similar to those reported by Crawford *et al.* (1999) for African Penguins at Robben Island over a whole breeding season (one year period). The proportion of birds that re-laid within five months of success or failure increased to 60% for birds that successfully reared chicks (second clutches), 60% for nests which failed during the incubation period, and 54% for nests which failed at the chick stage. These three proportions are approximately double the respective figures reported for birds at Robben Island over an entire breeding season: 21%, 32% and 23% (Crawford *et al.* 1999). At Marcus Island (33°02'S, 17°58'E), 12.3% of monitored nests comprised replacement clutches, and 5.8% were second clutches (La Cock & Cooper 1988). The higher frequency of replacement and second clutches at Dassen Island probably reflects the relatively high abundance of food during this study. At St. Croix Island (33°48'S, 25°46'E) in the Eastern Cape, the incidence of second clutches ranged from 76%, following the first breeding peak of the season, to 2% in the case of the second and third breeding peaks (Randall & Randall 1981).

In order to obtain a conservative estimate of the average number of chicks fledged per year, one can average the values for penguins recorded re-breeding within 2.5 months. This suggests that an average of 27% of breeders laid a second clutch. This figure would be the same for *Apollo Sea* and control nests because there were no significant differences between the *Apollo Sea* and control nests in either the median interval between egg failure and re-laying or between chick failure and re-laying. The mean number of chicks fledged per year would therefore be 1.13 (0.89 × 1.27) for all penguins, 1.20 (0.95 × 1.27) for control birds and 1.05 (0.83 × 1.27) for de-oiled *Apollo Sea* birds (Table 5.3 contains the figures for the mean number of chicks fledged per attempt). Although the re-breeding estimate is likely to be conservative for the duration of my study, it is important to note that my study was conducted during a period of increased

food availability. The proportion re-breeding, especially after successful breeding attempts (i.e. double brooding), would likely be of lower magnitude during periods of food scarcity.

In Humboldt Penguins *Spheniscus humboldti* 58% of birds successfully raise two broods within a year (Paredes *et al.* 2002). This high incidence of double-brooding is thought to be a strategy to maximise reproductive output in a highly productive, but unpredictable environment (Paredes *et al.* 2002, 2003). Given the similar environmental conditions experienced by the African Penguin (both breed in upwelling systems), and the similarities in foraging regimes (both being inshore foraging species), this strategy seems likely also to apply to African Penguins. Previously, it was thought that Humboldt Penguins double brood more frequently than African Penguins due to the greater incidence of El Niño perturbations and the more variable environment of the Humboldt system compared with the Benguela (Crawford *et al.* 2006a). Although this may be the case overall, the results from my study have shown that African Penguins have the ability, when conditions are favourable, to double brood at a similar frequency to Humboldt Penguins. Replacement clutches also form part of the Galapagos Penguin breeding phenology, giving rise to extended breeding seasons (Boersma 1976). The Magellanic Penguin, the only remaining species in the genus, is strictly seasonal, and so does not display the same degree of reproductive plasticity in response to varying food abundance (Boersma *et al.* 1990).

Incubation and hatching success

In general, variables relating to incubation and hatching success showed greater between-study effects than between-group effects, indicating that there was little difference between de-oiled *Apollo Sea* birds and un-oiled control birds. The mean clutch size was also similar for *Apollo Sea* and control nests. The mean clutch size for all nests (1.94) was slightly larger than previous figures reported for African Penguins at Robben Island (1.86) (Crawford *et al.* 1999), the Boulders (34°11'S, 18°27'E) (1.79) (Crawford *et al.* 2000) and in Namibia (1.84) (Kemper 2006). The slightly larger mean clutch size in this study suggests that few eggs were lost from a clutch before monitoring began, and may also have been influenced by the relatively high availability of food, especially during the second half of the study. The similarity in hatching success between the *Apollo Sea* and control groups suggests that for those penguins that did

breed, oil contamination did not negatively impact the hatchability of eggs. This suggestion is reinforced by the similar hatching masses of chicks from *Apollo Sea* and control nests.

Previous studies assessing the impact of oil contamination on the hatching success of bird eggs have produced contrasting results. Some have demonstrated reduced hatching of eggs that were oiled directly by investigators or by transfer from contaminated adults (Albers 1978, 1983, Ainley *et al.* 1981, Lewis & Malecki 1984, Parnell *et al.* 1984). In these cases, the reduced hatching of eggs is likely a result of altered metabolism and increased mortality of embryos due to systemic toxicity (Grau *et al.* 1977). Because the rehabilitated African Penguins monitored in this study were de-oiled, external transfer of oil to eggs from the breeding birds would not have taken place. However, other studies have shown embryotoxic effects when birds were orally dosed (e.g. Fry *et al.* 1986), presumably due to oil residues being incorporated into eggs during egg formation (Gorsline & Holmes 1982).

Butler *et al.* (1988) showed that both internal and external exposure of adult Leach's Storm-Petrels *Oceanodroma leucorhoa* to crude oils led to significantly reduced hatching success in a dose-dependent manner, and attributed this to the temporary desertion of the nest by the treated bird, rather than any toxic effects on the embryo. On the other hand, de-oiled Little Penguins did not exhibit reduced hatching success when compared with birds that had not been oiled in the two seasons following the *Iron Baron* oil spill (Giese *et al.* 2000). My results suggest that if there were any deleterious effects of oil contamination that may have impacted the hatchability of African Penguin, these were successfully "treated" in the de-oiling and treatment process at SANCCOB (for details of the treatment process, see Barrett *et al.* (1995), Parsons & Underhill (2005) and Dehrmann (2006)). This suggestion is further supported by the similar frequencies of infertile eggs from *Apollo Sea* and control nests. This finding is interesting in light of the inability of some of the *Apollo Sea* birds to breed following de-oiling (Chapter Two).

Fledging success

Although the observed fledging success of African Penguins was variable, the mean fledging success across all studies and study groups was higher than figures previously reported for the species. If one considers breeding success in terms of the number of

chicks fledged per breeding attempt, or per chick that hatched, both nests with one *Apollo Sea* adult and an *Apollo Sea* pair performed significantly worse than control nests. Overall, reproductive output of *Apollo Sea* nests was reduced by about 11%. The reduced productivity was greater for studies in which breeding success was relatively low (below the mean breeding success measured in this study), and less for those studies with above average breeding success. Indeed, in the studies with above average breeding success, the differences between the *Apollo Sea* and control group were negligible.

When one considers fledging success as the number of nests that fledged at least one chick, the results are slightly different. Using this definition, there was no difference between *Apollo Sea* nests and control nests. However, nests with two *Apollo Sea* birds had a significantly lower fledging success than all other nests. In contrast to some other studies (e.g. Butler *et al.* 1988, Giese *et al.* 2000), this effect was not temporary, but was evident throughout the six-year study period, although as with the previous analysis, the magnitude of the differences between *Apollo Sea* and control nests was greater in studies with lower overall breeding success. The long-term effect of oiling on the reproductive output of African Penguins in this study agrees with the findings of Barham *et al.* (2007) for African Penguins oiled in the *Treasure* oil spill.

The difference in the results of these two approaches to fledging success can be attributed to the partial losses of chicks from a brood, which were accounted for in the first approach (number of chicks fledged per pair or per hatchling), but were ignored in the second (used in the generalized linear model to investigate the influence of explanatory variables). Of nests at which chicks hatched, 48% of control nests fledged two chicks, compared to 39% for *Apollo Sea* nests. These figures increase to 65% and 54% for control and *Apollo Sea* nests respectively when one restricts the analysis to successful nests. On the other hand, the *Apollo Sea* nests experienced partial losses of chicks from broods (hence rearing only one chick from a two chick brood) more frequently than control nests. The greater frequency of complete failures in nests with *Apollo Sea* pairs explains why this study group was found to perform significantly worse than control birds in both analyses. These results differ from those of a subset of the same data, analysed using less rigorous statistical methods and a smaller sample size (Wolfaardt & Nel 2003).

Fledging success and hatching success were correlated suggesting that similar factors influenced both of these parameters. The observation that only fledging success of *Apollo Sea* birds was reduced relative to control nests indicates that the impaired ability of *Apollo Sea* birds manifests during the energetically demanding chick-rearing period, rather than during incubation. African Penguin chicks face the greatest risk of dying in the first 10 days after hatching (Seddon & van Heezik 1991b, Kemper 2006), before they have attained full thermoregulatory capacity (Erasmus & Smith 1974). Chick mortality in this study largely conformed to this pattern. However, there were differences between study groups. Chick mortality from control nests decreased with age, consistent with other studies on African Penguins. On the other hand, a relatively high proportion of chicks from *Apollo Sea* nests, and especially those with two *Apollo Sea* adults, died when they were older than 40 days, indicating that chicks from this age group were more likely to die if they were from *Apollo Sea* nests. This was also the case with chicks raised by de-oiled African Penguins from the *Treasure* spill at Robben Island (Barham *et al.* 2007).

Seddon & van Heezik (1991b) have shown that there are two distinct stages of chick mortality in African Penguins. The first occurs from hatching to about 34 days of age, when chicks die mostly of exposure to predation and climatic variables (e.g. heavy rainfall, Randall *et al.* 1986), nest-related factors (e.g. the collapse of burrows) and by accident (e.g. chicks smothered by the brooding adult). The second stage of chick mortality occurs from 40–90 days after hatching, when deaths are almost exclusively due to starvation (Seddon & van Heezik 1991b). I therefore propose that the reduced fledging success in *Apollo Sea* nests is due to the increased mortality of chicks older than 40 days. I further propose that this increased mortality is due to an impaired ability of *Apollo Sea* birds to meet the energetic demands of their chicks, especially when the food demands of the chicks' peak, from about 40–70 days after hatching (Cooper 1977a, Bouwhuis *et al.* in prep). It is during this period that the greatest energetic demands will be placed on the breeding birds.

The increased failure of *Apollo Sea* nests at the late chick stage is likely due to increased nest desertion, reduced provisioning of chicks by *Apollo Sea* parents, or a combination of both of these possibilities. Oil-related reduction in fledging success of

Leach's Storm-Petrels was attributed to temporary desertion of nests by oil-dosed (both oral and external) parents (Butler *et al.* 1988). In a separate study, oiling was shown to impair the chick provisioning ability of adult Leach's Storm-Petrels (Trivelpiece *et al.* 1984). Sub-lethal oiling of adult South Polar Skuas *Catharacta maccormicki* following the *Bahia Paraiso* oil spill in Antarctica is thought to have led to the temporary abandonment of nests by contaminated birds, thereby exposing chicks to increased intraspecific predation of chicks (Eppley & Rubega 1989, 1990, but see Trivelpiece *et al.* 1990).

In Magellanic Penguins, body condition (body mass) of the parents at the beginning of the incubation period is the most important determinant of nest desertions (Yorio & Boersma 1994). Birds in poor condition (lower lipid reserves) display a lower tolerance to fasting during the relatively long incubation spells and are thus more likely to abandon nests than birds in better condition. Magellanic Penguins have incubation shifts of one to three weeks (Boersma *et al.* 1990), much longer than the incubation shifts for African Penguins, which are generally less than five days and average 1.1 days for eggs hatched successfully (Williams & Cooper 1984). Body condition of African Penguins at the onset of incubation may not, therefore, be as critical a determinant of nest desertion as is the case for Magellanic Penguins. However, it is still likely to influence nest desertion rates, especially when the environmental conditions, such as food availability, are poor, thereby placing the bird under additional stress. Exactly how oil contamination would affect the body condition of African Penguins is unclear. Experimental studies of other seabirds indicate that there is often long-term damage to key organs, especially the liver and kidney, as a result of the ingestion of even small quantities of oil (Fry & Lowenstine 1985). Such damage can lead to the disruption of many aspects of the birds' physiology (Miller *et al.* 1978, Peakall *et al.* 1981, Gorsline & Holmes 1982, Nisbet 1994), that may in turn influence body condition. Oil contaminated penguins are thought to experience a greater cost of reproduction than un-oiled birds (Giese *et al.* 2000, Goldsworthy *et al.* 2000, Chapter Two), suggesting that these birds are in poorer condition than un-oiled birds. The cost exerted by reproducing on de-oiled birds may in itself further influence body condition and subsequent breeding performance.

Oiling has also been shown to reduce the fledging success of Little Penguins, predominantly as a result of reduced reproductive output from nests with de-oiled females (Giese *et al.* 2000). Similarly, female Magellanic Penguins appear to suffer a

greater energetic cost when oiled than males (Fowler *et al.* 1995). I did not detect any differences in reproductive output between sexes in de-oiled African Penguins from the *Apollo Sea* spill. My results suggest that both sexes were impacted, and that the impacts were additive in pairs (nests) with two *Apollo Sea* birds. Male and female African Penguins share incubation and chick provisioning responsibilities equally (Rand 1960). Deleterious impacts on the condition or fitness of both members of a pair would therefore be expected to reduce reproductive output more than if only one member of a pair was affected.

Chick Growth

Fledging success is a useful measure of breeding productivity, but doesn't provide information about the quality of the chicks produced. The chick-rearing period is the most demanding of the breeding cycle for seabirds (Ricklefs 1983). Chick growth is a measurement that integrates the foraging abilities of both parents. A detectable result at this level would therefore suggest differences in the provisioning capabilities (and therefore fitness) of one or both parents. Previous studies of chick growth in *Spheniscus* penguins indicate that growth rates of chicks in the wild are constrained by food availability; the growth rates of hand-reared chicks are significantly faster than those of chicks in the wild, and patterns of growth in the wild tend to reflect food availability (Cooper 1977a, 1980, Randall 1983, Wilson 1985, Boersma *et al.* 1990, Hennicke & Culick 2005).

The significant variability in African Penguin chick growth rates in this study is thought to be due, at least partly, to changes in the abundance of available food. Studies in which chick growth was depressed tended to be those with low breeding success. On the other hand, faster growth rates were found in studies with high breeding success, which in turn was correlated with increases in estimates of the biomass of the dominant fish prey of African Penguins. Even within studies, the growth rates of chicks fluctuated around the mean for the entire study, indicating that growth of African Penguin chicks is highly sensitive to the factors which influence it.

Successful chicks (i.e. those which fledged) had significantly faster growth rates than chicks which were unsuccessful, suggesting that many of the chicks which did not fledge died as a result of depressed growth rates, or starvation. Singletons and A-chicks grew

at similar rates, but B-chicks grew significantly slower than both singletons and A-chicks. For chicks which died the magnitude of the differences was much greater; in this case, A-chicks grew significantly slower than singletons, and B-chicks performed worst of all. This result is not surprising given that chick growth is limited by available food. Consequently, singletons would generally be expected to receive more food than chicks from a two-chick brood, especially when food supply is poor. The similar growth rates of successful singletons and A-chicks seems counterintuitive, but a similar result was reported by van Heezik & Seddon (1991) for African Penguin chicks in a study which took place at Dassen Island during poor feeding conditions. van Heezik & Seddon (1991) suggested that the lack of difference in growth rates between chicks from one- and two-chick broods in their study may have been due to parents of two-chick broods increasing their provisioning response to an increased begging stimulus from two-chick broods, or from the age and experience of parents (parents of one-chick broods possibly being less experienced and more likely to lay infertile eggs). van Heezik & Seddon (1991) also found that as a group A-chicks grew at a similar rate to B-chicks, but within a brood, B-chicks grew significantly slower. Within-brood differences have also been reported by Williams & Cooper (1984). The detection of overall differences between A- and B-chicks in this study may be due to the much larger sample size (over 900 chicks were weighed) than the van Heezik & Seddon (1991) study, in which 90 chicks were weighed. Differences in growth rates between A- and B- chicks have also been reported for Galapagos Penguins *Spheniscus mendiculus* (Boersma 1976) and Adélie Penguins *Pygoscelis adeliae* (Taylor 1962). The difference in growth rates between A- and B-chicks can be explained by the effects of hatching order and sibling asymmetries. Direct competition occurs between chicks of a brood, and results in the larger, first-hatched A-chick receiving more uninterrupted feeds than the B-chick (Seddon & van Heezik 1991a, van Heezik & Seddon 1996).

The chicks of de-oiled African Penguins grew significantly slower than chicks from other study groups, but only when the pair comprised two *Apollo Sea* parents. This effect was most noticeable when the growth rates of chicks were below the average for the study, which is consistent with the patterns of fledging success. This pattern suggests that when feeding conditions are good de-oiled birds are compromised less relative to un-oiled birds than when feeding conditions are poor. When feeding conditions deteriorate, birds in poor condition would be less able to sustain the energetic demands of their

chick(s) leading to both reduced growth rates and increased mortality of chicks. Chick growth in nests with one *Apollo Sea* parent, whether male or female, was similar to un-oiled birds, suggesting that the un-oiled partner may partially compensate for the effects of oiling in its partner, or that individuals vary in their ability to provision chicks. Underhill *et al.* (1999) report that an individual penguin on Robben Island was able to raise two chicks by itself after its mate was removed from the study nest because it was oiled during the *Apollo Sea* spill. A similar incident, involving a single adult raising a chick alone after the Cape Town Harbour spill of May 1998, was reported by Whittington (2000). These are likely to be exceptional cases, but illustrate the resilience and remarkable performance of some individuals in rearing chicks.

The temporal variability in the oiling effect on chick growth, and the observation that it manifests predominantly in nests with two de-oiled birds suggests that the reduced growth of chicks was not due to secondary poisoning of the embryo, as has been reported for some other species (Miller *et al.* 1978, Peakall *et al.* 1980). The oiling effect in my study is more likely due to an impaired ability of de-oiled birds to meet the energetic demands of their chicks, as was proposed for oiled Leach's Storm-Petrels (Trivelpiece *et al.* 1984), and de-oiled Little Penguins (Giese *et al.* 2000).

Mate fidelity

One of the factors which may have contributed towards the reduced breeding performance of de-oiled *Apollo Sea* birds compared with control birds was the disruption of pair bonds. Most seabirds are monogamous, although there is variation in the degree of mate fidelity both within and among species (Lack 1968, Choudhury 1995, Bried *et al.* 1999, Bried & Jouventin 2002). Penguins have generally been considered a classic example of a taxon with a primarily monogamous breeding system. Among penguins, inshore foragers, such as the African Penguin, are predicted to exhibit relatively high mate fidelity (Croxall & Davis 1999). Evidence for positive associations between mate fidelity and subsequent breeding success has been reported for many seabird species (e.g. Mills 1973, Ollason & Dunnet 1988, Bradley *et al.* 1995, Harris *et al.* 1996, St. Clair *et al.* 1999, Bried *et al.* 2003).

Studies of African Penguins indicate an annual fidelity rate of between 80% and 94% under "normal" circumstances (Randall 1983, Crawford *et al.* 1995). Thus, mate

retention appears to be the optimum breeding strategy for African Penguins, presumably to avoid the potentially high costs of obtaining a new mate, including a reduction in the reproductive output with a new mate and missed breeding opportunities between divorce and re-mating (Williams & Rodwell 1992, McNamara & Forslund 1996, Croxall & Davis 1999, Bried & Jouventin 2002, Bried *et al.* 2003, Mills & Ryan 2005).

The re-unite rate of 87.5% for un-oiled control birds in this study accords with previous estimates for African Penguins. That the re-unite rate of de-oiled *Apollo Sea* birds (64.8%) was significantly lower than the control group indicates that oiling and the de-oiling process disrupted the maintenance of pair bonds of de-oiled birds. The higher level of mate switching in *Apollo Sea* birds is likely to result in reduced mate "confidence" and synchrony relative to partners in control pairs. Oiling can disrupt established pair bonds in several ways. The death of some birds in the oil spill would result in the loss of mates. The different lengths of time that birds spent at SANCCOB, and individual differences in the period to restoration (delayed breeding) due to sub-lethal and physiological impacts of oiling (Chapter Two), would result in the breeding and moult cycles of some established pairs being disrupted and thus becoming asynchronous (Underhill & Crawford 1999, Hemming 2001, Chapters Three & Four). On the other hand, the disruption of pair bonds brought about by the oil spill may have contributed towards the delay in breeding by de-oiled *Apollo Sea* birds subsequent to their release (Chapter Two). Resident birds that were not oiled in the spill would also be expected to have experienced some disruption to pair bonds, although to a lesser degree than oiled birds, especially if their mates were oiled in the spill. It is thus noteworthy that un-oiled control birds on Dassen Island had a similar rate of mate fidelity compared with the situation in "normal" periods (i.e. without oil spills). This suggests the possible impact of additional, confounding factors. Mate fidelity may for example be influenced by the quality or breeding performance of a bird (Perrins & McCleery 1985). Higher rates of divorce in unsuccessful breeding pairs have been recorded for King Penguins *Aptenodytes patagonicus* (Olsson 1998) and Fiordland Crested Penguins *Eudyptes pachyrhynchus* (St. Clair *et al.* 1999). This was also the case for African Penguins in my study, which were more likely to re-unite with their previous mate following a successful breeding attempt than a failed breeding attempt. The lower breeding success of de-oiled *Apollo Sea* birds may therefore in itself have contributed towards increased mate switching relative to control birds. In addition, reproductive output of birds that re-united

was significantly greater than birds which divorced and switched mates. Although mate fidelity was influenced by prior breeding success, and also influenced subsequent breeding success, these factors alone could not account for the total reduction in reproductive output of de-oiled *Apollo Sea* birds relative to control birds. Additional factors, such as the sub-lethal impacts discussed earlier and in Chapter Two, are likely also to have contributed towards the reduced breeding success of *Apollo Sea* birds. More research is required to understand better the cause-effect relationships between oiling, mate fidelity and breeding success.

Inter-colony comparisons

The lower fledging success and chick growth rates in Area B compared to Area G is difficult to explain. It is tempting to suggest that these differences may relate to differences in the food available to these two colonies on Dassen Island, but this seems unlikely. Breeding birds from Dassen Island, fitted with satellite transmitters, have been tracked to the Boulders colony and the entrance of False Bay, about 130km away (Crawford & Whittington 1997, Petersen *et al.* 2006). It is unlikely then that birds from different colonies on Dassen Island (Area G and B are less than 2km apart) would experience different foraging conditions over the same time period. Ectoparasites reduce fledging success in some seabirds (Feare 1976). Ticks and other ectoparasites are potential transmitters of viruses, which may compromise the health of chicks and even result in fatalities (Nuttall 1984), thereby potentially reducing both chick growth and fledging success. The moisture content of nesting material has been found to influence the number of ticks in African Penguin nests (Daturi 1986). It is possible that subtle differences in the substrate and vegetation composition of these two areas may have resulted in there being larger numbers of ticks in Area B, but I do not have any data to test whether this is the case.

Breeding success of African Penguins at Robben Island is also known to be significantly influenced by the abundance of pelagic fish (Crawford *et al.* 1999). The increased availability of Anchovy and Sardine experienced in the second half of this study, also resulted in improved breeding success of penguins at Robben Island (Crawford *et al.* 2006b). The improved breeding success of Robben Island birds (mean value of 0.73 chicks per pair when the combined spawner biomass of their fish prey was above two million tons, Crawford *et al.* 2006b) was still lower than the mean breeding success for

penguins at Dassen Island during this study (0.89), suggesting that breeding success is generally higher at Dassen Island than Robben Island. Crawford *et al.* (2006b) found that the abundance of food accounted for 40% of the variation in breeding success at Robben Island between 1989 and 2004 and suggested that other factors, such as the quality of nesting habitat and predation by Feral Cats *Felis catus* also contribute towards breeding success. The Feral Cat population at Dassen Island (Cooper 1977b) has been eradicated (J. Visagie pers. comm.), which could at least partly explain differences in breeding success between these two colonies. Furthermore, nests used in my study were exclusively burrows, which are known to be amongst the most successful nest types for African Penguins (Frost *et al.* 1976, Seddon & van Heezik 1991b, Murison 1998); a range of nest types formed part of the Robben Island study (R.J.M. Crawford, pers. comm.). Lastly, Robben Island penguins would have been exposed to a much greater degree of human disturbance than penguins from Dassen Island as a result of the large number of tourists visiting the island and the larger permanent human population that live and work there. Human disturbance is known to affect breeding African Penguins adversely, both behaviourally (Hockey & Hallinan 1981) and physiologically (M. Giese and M.S. de Villiers *in litt.*) and so may contribute towards reduced breeding success.

Individual variation in breeding success

There was evidence in this study of individuals which performed consistently well and others which performed poorly. S0575 was originally treated at SANCCOB (although not for oiling), and released at Robben Island in September 1989. It was re-sighed on Dassen Island in March 1994, and came ashore oiled on Robben Island in the *Apollo Sea* oil spill. After its release from SANCCOB it returned to Dassen Island, and was found oiled there again in August 1995. This bird was monitored in two breeding studies in 1996 and 1997, and on both occasions the chicks failed to hatch. After these two attempts, S0575 was observed on two further occasions (not breeding) and was never observed again after March 1998, and was presumed to have died. On the two occasions it did attempt to breed, its mate was S21225, also an *Apollo Sea* survivor. This bird was included in 10 of the breeding success studies, two with S0575 as its mate, and failed to produce hatchlings in all except two of the studies. On the other hand, the pair comprising S22061 and S22954 (both *Apollo Sea* survivors) were monitored in five of the breeding success studies and were successful in fledging at

least one chick in all five of these attempts. The performance of this pair is even more remarkable in light of the relatively poor performance of nests with *Apollo Sea* pairs.

Individual variation in reproductive success has been attributed to age and experience in many studies (Ainley *et al.* 1983, Wooller *et al.* 1992, Forslund & Part 1995), and may have contributed, at least partly, to variability in breeding success between individuals in this study. It is also possible that individuals varied in the degree to which they were affected by the original oil contamination. The key factor affecting the post-release survival of de-oiled Little Penguins was the original extent of oiling and its influence on mass and body condition (Goldsworthy *et al.* 2000). These parameters were not measured in my study. However, body mass at capture has been found to influence significantly the mortality rates of oiled African Penguins; birds in poor condition (< 2kg) suffer a significantly greater mortality rate than those heavier than 2kg at capture (Kerley & Erasmus 1987). The body condition of birds at capture may therefore influence the long-term reproductive success of affected birds.

Potential impact of flipper-bands on breeding success

Several authors have raised concerns about the potential impacts of flipper-bands on penguins and the possible bias of data collected from flipper-banded birds (Culik *et al.* 1993, Stonehouse 1999, Jackson & Wilson 2002, Petersen *et al.* 2005). The energetic and life-history impacts of flipper-bands on penguins vary from species to species, and according to the band material and design (Culik *et al.* 1993, Hindell *et al.* 1996, Jackson & Wilson 2002, Gauthier-Clerc *et al.* 2004, Petersen *et al.* 2005). A batch of about 70 de-oiled *Apollo Sea* birds had their bands fitted too tightly, some of which suffered injuries resulting from the constriction of the base of the flipper (Underhill 1995). Tight bands were removed from birds that had not yet been released from SANCCOB, and also from birds that were observed with tight-fitting flipper-bands on Dassen Island. A temporary moratorium was placed on the use of flipper-bands following this incident. Consequently, I was unable to band the control birds in the study. Because most of the un-oiled birds were unbanded, it could be argued that the differences in breeding success and chick growth rates between de-oiled birds and the unaffected (control) birds may have been in part due to potential effects of the flipper-bands. However, in a five-year study (2001–2005) of African Penguins at Robben Island following the *Treasure* oil spill, the breeding success of banded penguins was indistinguishable from that of unbanded penguins

(Barham *et al.* 2007). This result suggests that flipper-bands do not adversely affect the breeding success of African Penguins. Thus, the difference in breeding success between de-oiled and un-oiled birds in this study can be attributed to the impacts of oiling, and not due to potential band effects.

CONCLUSION

The results of this study provide evidence that oil contamination adversely affects the long-term reproductive performance of African Penguins. These impacts manifest mostly during the chick rearing period, especially when feeding conditions deteriorate. The reduction in reproductive output is exacerbated in nests with two de-oiled birds. The study was conducted during a period of increasing food availability, which resulted in a high overall breeding success, and may have partly offset some of the potential oiling impacts. Indeed, although the reproductive performance of *Apollo Sea* nests (0.83 chicks fledged per breeding attempt or 1.05 chicks per year) was less than control nests, the productivity of *Apollo Sea* nests was higher than most previous estimates of breeding success for African Penguins. Together with the results from Chapter Two, there is clear support for the continued capture, de-oiling and release of oiled African Penguins on conservation grounds. These results also suggest that if the study was conducted during a period of much poorer food availability, the reproductive performance of the de-oiled birds would likely have been substantially lower. With this in mind, it is important that future oil spill survivors continue to be monitored as part of the rehabilitation process. The results also highlight the importance of reducing the incidence of spills so that birds do not become contaminated in the first place. Finally, management of the pelagic fish resource in a manner that accounts for the needs of African Penguins and other marine predators is critical for the conservation of the species.

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Table 5.1 Periods over which breeding success studies of African Penguins were conducted at Dassen Island and sample sizes of study groups.

Study Number	Study period	*Apollo Sea* nests (*n*)	Control nests (*n*)
1	22/9/1994-7/4/1995	72	48
2	09/3/1995-24/7/1995	82	75
3	27/05/1995-8/09/1995	16	17
4	17/07/1995-1/11/1995	27	34
5	18/10/1995-12/02/1996	21	16
6	18/03/1996-13/08/1996	56	49
7	24/05/1996-21/10/1996	40	36
8	1/08/1996-4/01/1997	35	34
9	15/11/1996-10/03/1997	49	43
10	15/04/1997-04/08/1997	38	42
11	23/06/1997-9/11/1997	37	30
12	21/09/1997-7/02/1998	35	37
13	29/12/1997-6/05/1998	35	29
14	16/04/1998-2/08/1998	33	32
15	20/07/1998-30/11/1998	44	35
16	11/01/1999-8/06/1999	48	34
17	10/05/1999-5/10/1999	64	40
18	10/10/1999-16/02/2000	35	67
TOTAL		767	698

Table 5.2 Explanatory variables tested in generalized linear models of breeding success for African Penguins at Dassen Island.

Study	Study 1 – 18
Area	Area G or B
Rehab2	Rehab Group[1] with two levels: Codes 1, 2, 3 vs Code 4
Rehab3	Rehab Group[1] with three levels: Codes 1, 2 vs Codes 3, 4
tRehab	Factor to test for trends in relative performance of rehab birds
Rehab2.Study	Interaction between nests with *Apollo Sea* pairs and Study
Month	Egg laying month
sYear cYear s2Year c2Year	Periodic terms used to test whether there is a smooth pattern of seasonality in breeding success, as used for example by Underhill *et al.* (1992), Harrison *et al.* (1997) and Kemper (2006)
[1] Rehab Group Codes	1 - Control nest 2 - Nest with an *Apollo Sea* male 3 - Nest with an *Apollo Sea* female 4 - Nest with an *Apollo Sea* male and female (i.e. pair)

Table 5.3 Summary of breeding success parameters for African Penguins in the different study groups at Dassen Island

Breeding Parameter	Control	*Apollo Sea* All	*Apollo Sea* Pairs	All nests
Number of nests	698	767	138	1465
Mean clutch size ± SD	1.95 ± 0.23	1.93 ± .26	1.92 ± 0.27	1.94 ± 0.24
Number of eggs hatched	975	1006	195	1981
Hatching Success (%)	71.69	67.79	73.58	69.66
Number chicks fledged	661	641	113	1302
Fledging Success (%)	67.79	63.72	57.95	65.72
Total successful nests[1]	400	415	72	815
Mean fledging period for successful chicks	72.71 ± 11.72	72.74 ± 11.40	72.95 ± 12.17	72.73 ± 11.55
Mean chicks fledged per nest ± SD	0.95 ± 0.87	0.83 ± 0.85	0.82 ± 0.86	0.89 ± 0.87

[1] Nests fledging at least one chick

Table 5.4 Proportions of nests with successful two-chick broods, partial failures and complete failures for different study groups of African Penguins at Dassen Island. The results are restricted to those nests at which eggs hatched to minimise bias associated with not having followed nests from egg-laying.

		Number of nests fledging 0, 1 or 2 chicks[1]					
Study Group	Number of nests[1]	1 hatched, 0 fledged	1 hatched, 1 fledged	2 hatched, 0 fledged	2 hatched, 1 fledged	2 hatched, 2 fledged	Mean no. chicks fledged per nest ± SD[1]
Control	543	42 (7.7%)	70 (12.9%)	101 (18.6%)	69 (12.7%)	261 (48.0%)	1.22 ± 0.84
Apollo Sea All	574	59 (10.3)	84 (14.6%)	100 (17.4%)	105 (18.3%)	226 (39.4%)	1.12 ± 0.81
Apollo Sea Pairs	110	12 (10.9%)	13 (11.8%)	26 (23.6%)	18 (16.4%)	41 (37.3%)	1.03 ± 0.85

[1]Only nests at which chicks hatched are included

Table 5.5 Age categories at which African Penguin chicks died in different study groups at Dassen Island.

Age class at death	Control (n = 313)	*Apollo Sea* All (n = 364)	*Apollo Sea* Pairs (n = 82)
≤ 5 days	96	91	7
6–40 days	179	190	50
> 40 days	38	83	22

Table 5.6 Results of the generalized linear model of the parameter λ of an exponential distribution for incubation success of African Penguins at Dassen Island. Study is the only explanatory variable, and the regression coefficients are in relation to Study 6. Negative values for the coefficients indicate smaller values of λ, which translate into higher values of incubation success (see text for further details).

Explanatory variable	Regression coefficient	SE	*t*
Constant	– 4.853	0.3	– 16.15
Study 1	– 0.76	0.538	– 1.41
Study 2	0.744	0.357	2.09
Study 3	1.992	0.396	5.03
Study 4	1.157	0.382	3.03
Study 5	0.36	0.449	0.8
Study 6	0		
Study 7	1.065	0.361	2.95
Study 8	0.654	0.378	1.73
Study 9	0.649	0.371	1.75
Study 10	0.523	0.382	1.37
Study 11	0.4	0.382	1.05
Study 12	0.315	0.386	0.82
Study 13	– 0.441	0.482	– 0.91
Study 14	0.736	0.426	1.73
Study 15	0.489	0.382	1.28
Study 16	– 0.591	0.48	– 1.23
Study 17	– 0.022	0.375	– 0.06
Study 18	0.115	0.382	0.3

Table 5.7 Results of the generalized linear model of the parameter λ of an exponential distribution for fledging success of African Penguins at Dassen Island in relation to three explanatory variables: Study, Area and Rehab Group. The coefficients for studies are in relation to Study 6, the coefficient for Area in relation to Area G, and the coefficient for Rehab Group in relation to Rehab codes 1, 2 and 3 combined (i.e. all nests except those with *Apollo Sea* pairs). Negative values for the coefficients indicate smaller values of λ, which translate into higher values of fledging success (see text and Underhill (submitted) for further details).

Explanatory variable	Regression coefficient	SE	*t*
Constant	– 5.779	0.285	– 20.29
Study			
Study 6	0		
Study 1	0.179	0.409	0.44
Study 2	1.101	0.332	3.32
Study 3	0.885	0.434	2.04
Study 4	– 0.084	0.409	– 0.2
Study 5	0.673	0.424	1.59
Study 7	0.787	0.349	2.25
Study 8	– 0.091	0.41	– 0.22
Study 9	– 0.158	0.378	– 0.42
Study 10	– 0.135	0.41	– 0.33
Study 11	– 0.097	0.409	– 0.24
Study 12	– 0.686	0.467	– 1.47
Study 13	– 0.845	0.492	– 1.72
Study 14	0.225	0.383	0.59
Study 15	– 0.495	0.42	– 1.18
Study 16	– 0.189	0.378	– 0.5
Study 17	– 0.416	0.385	– 1.08
Study 18	– 0.431	0.392	– 1.1
Area			
Area G	0		
Area B	0.383	0.136	2.81
Rehab Group			
Control nests and nests with one *Apollo Sea* individual	0		
Nests with an *Apollo Sea* pair	0.469	0.191	2.45

Table 5.8 Modelled probability of African Penguin nests at Dassen Island successfully fledging at least one chick. See Table 5.7 for the regression coefficients used to calculate the probability of success and the text for details of the calculations.

	Area G		Area B	
Study	All nests	*Apollo Sea* Pairs	All nests	*Apollo Sea* Pairs
1	0.76	0.65	0.67	0.53
2	0.50	0.33	0.36	0.20
3	0.57	0.41	0.44	0.27
4	0.81	0.71	0.73	0.61
5	0.64	0.49	0.49	0.35
6	0.80	0.69	0.73	0.58
7	0.61	0.45	0.48	0.31
8	0.81	0.72	0.74	0.61
9	0.82	0.73	0.75	0.63
10	0.82	0.73	0.75	0.63
11	0.81	0.72	0.74	0.61
12	0.89	0.83	0.84	0.76
13	0.91	0.85	0.87	0.79
14	0.75	0.63	0.66	0.51
15	0.87	0.80	0.82	0.72
16	0.83	0.74	0.76	0.64
17	0.86	0.79	0.80	0.70
18	0.86	0.79	0.80	0.71

Table 5.9 Multiple regression model coefficients for mean z-values (standardized growth rates) per African Penguin chick at Dassen Island in relation to explanatory variables. The coefficients are in relation to the following reference levels: Study 1, Area B, Success (i.e. chick fledged), Singleton broods, and Rehab codes 1,2 and 3 combined (i.e. all nests except those with *Apollo Sea* pairs). Negative values indicate lower growth rates. *P* values of < 0.05 are in bold.

Explanatory variable	Regression coefficient	SE	*t* (931)	*P* value
Constant	– 0.0218	0.0841	– 0.26	0.795
Study				
Study 1	0			
Study 2	– 0.201	0.073	– 2.74	**0.006**
Study 3	0.139	0.094	1.48	0.139
Study 4	0.056	0.076	0.75	0.456
Study 5	0.116	0.082	1.41	0.159
Study 6	0.216	0.072	3	**0.003**
Study 7	– 0.088	0.074	– 1.18	0.24
Study 8	0.114	0.073	1.55	0.121
Study 9	0.128	0.075	1.72	0.086
Study 10	0.380	0.070	5.45	**< 0.001**
Study 11	0.247	0.073	3.38	**< 0.001**
Study 12	0.244	0.070	3.48	**< 0.001**
Study 13	0.251	0.069	3.63	**< 0.001**
Area				
Area B	0			
Area G	0.146	0.030	4.79	**< 0.001**
Success/Fail (chicks fledged or failed)				
Success	0			
Fail	– 0.235	0.08	– 0.93	**0.003**
Brood type				
Singleton	0			
A-chick	0.004	0.051	0.07	0.946
B-chick	– 0.107	0.053	– 2.03	**0.043**
Brood type - Success/Failure interaction (See Table 5.10 for further details)				
Failure - Singleton	0			
Failure - A - chick	– 0.189	0.094	– 2.02	**0.044**
Failure - B - chick	– 0.375	0.093	– 4.05	**< 0.001**
Rehab code/Study group				
Control nests; nests with individual *Apollo Sea* parents	0			
Nests with *Apollo Sea* pairs	– 0.051	0.031	– 1.65	**0.0495***

* One-tailed test

Table 5.10 Regression coefficients of mean z-value (standardized growth rates) per African Penguin chick at Dassen Island for interactions between Brood Type and whether a chick fledged or failed. Negative values indicate lower growth rates.

	Chick Fledged (Success)	Chick Failed (Failure)	
Singleton	0	– 0.235	
A-chick within a brood	0.004	– 0.420	(– 0.235 + 0.004 – 0.189)
B-chick within a brood	– 0.107	– 0.717	(– 0.235 – 0.107 – 0.375)

Table 5.11 The number of times which de-oiled *Apollo Sea* and un-oiled (control) African Penguins at Dassen Island re-united with previous partners, or re-paired with another individual, either while both partners were still alive (divorce), or as a result of the death of the previous partner (widow), 1995-2000. See text for further information and for definitions of these terms.

	Re-unite		Divorce		Widow	
	n	%	n	%	n	%
Apollo Sea birds	112	64.8	61	35.3	21	10.8
Control birds	35	87.5	5	12.5	3	6.9

Table 5.12 Modelled probabilities of de-oiled and un-oiled (control) African Penguins at Dassen Island re-uniting with their mates following a successful or failed breeding attempt, 1995-2000. A successful breeding attempt was one in which at least one chick was reared to fledging.

Outcome of prior breeding attempt	All birds	*Apollo Sea*	Control
Failed	0.525	0.520	0.757
Successful	0.836	0.804	0.922

Table 5.13 Modelled probabilities of de-oiled and un-oiled (control) African Penguins at Dassen Island successfully rearing a chick dependent on whether they divorced and re-paired with a new mate, or re-united with their previous mate, 1995-2000.

	All birds	*Apollo Sea*	Control
Divorce	0.515	0.507	0.671
Re-unite	0.705	0.678	0.806

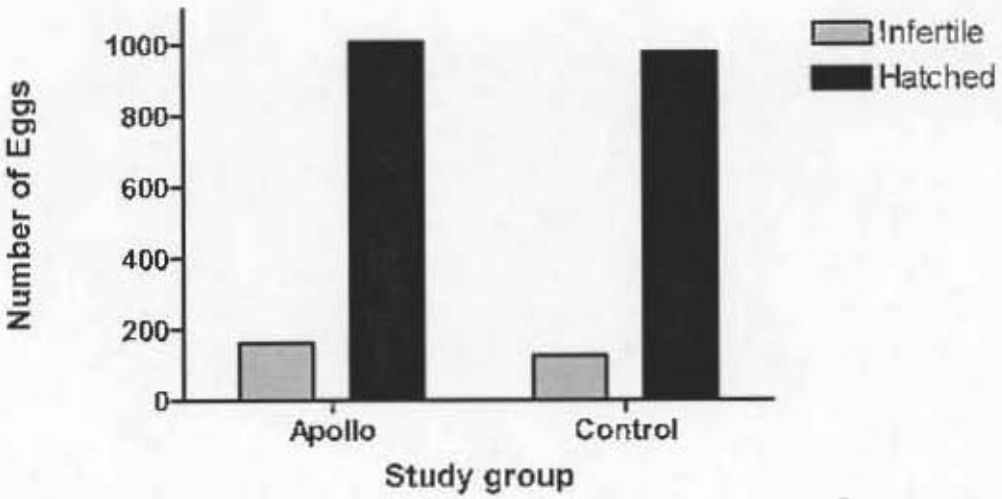

Figure 5.1 The number of infertile versus successfully hatched eggs from African Penguin nests across all studies at Dassen Island, 1994-2000.

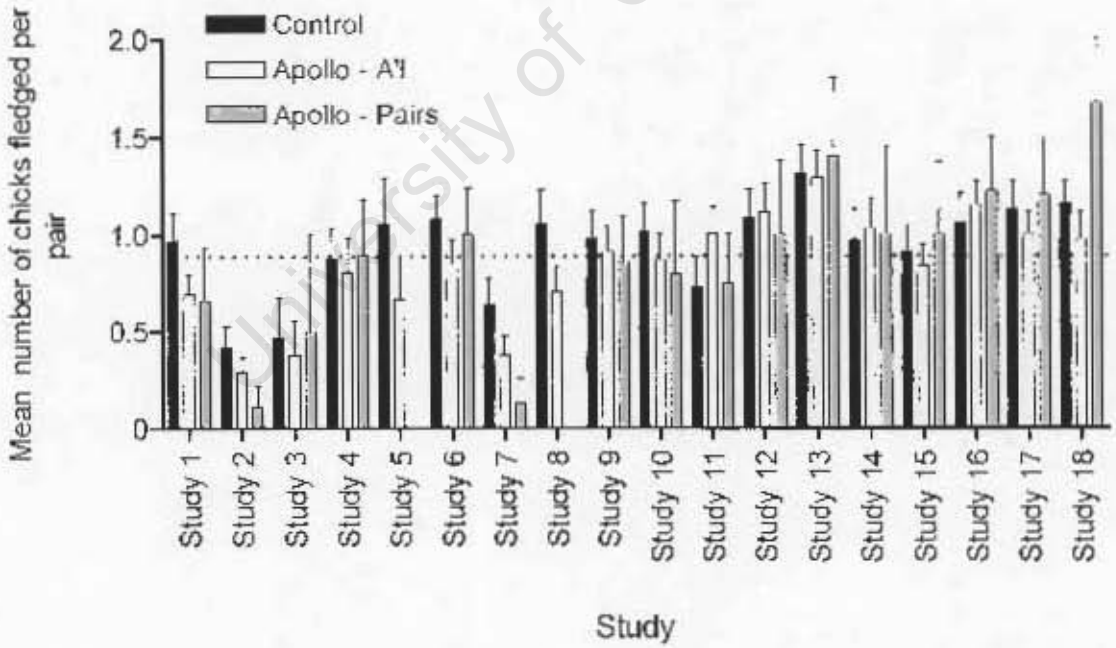

Figure 5.2 Breeding success of African Penguins at Dassen Island measured as the mean number of chicks fledged per pair in each of the 18 studies, for *Apollo Sea* and control nests. Error bars represent the SE of the mean. The dotted line indicates the mean breeding success (chicks/pair/attempt) for all study nests over the entire study.

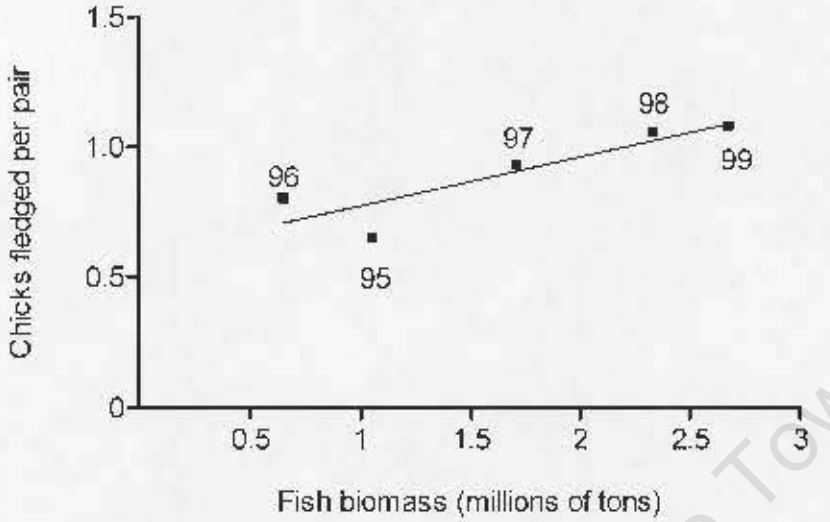

Figure 5.3 Relationship between breeding success (mean no. chicks fledged/pair/attempt) of African Penguins at Dassen Island and the combined biomass of Anchovy and Sardine, 1995-1999 (r = 0.886, P = 0.0227). The fish biomass estimates are from Marine and Coastal Management spawner biomass surveys.

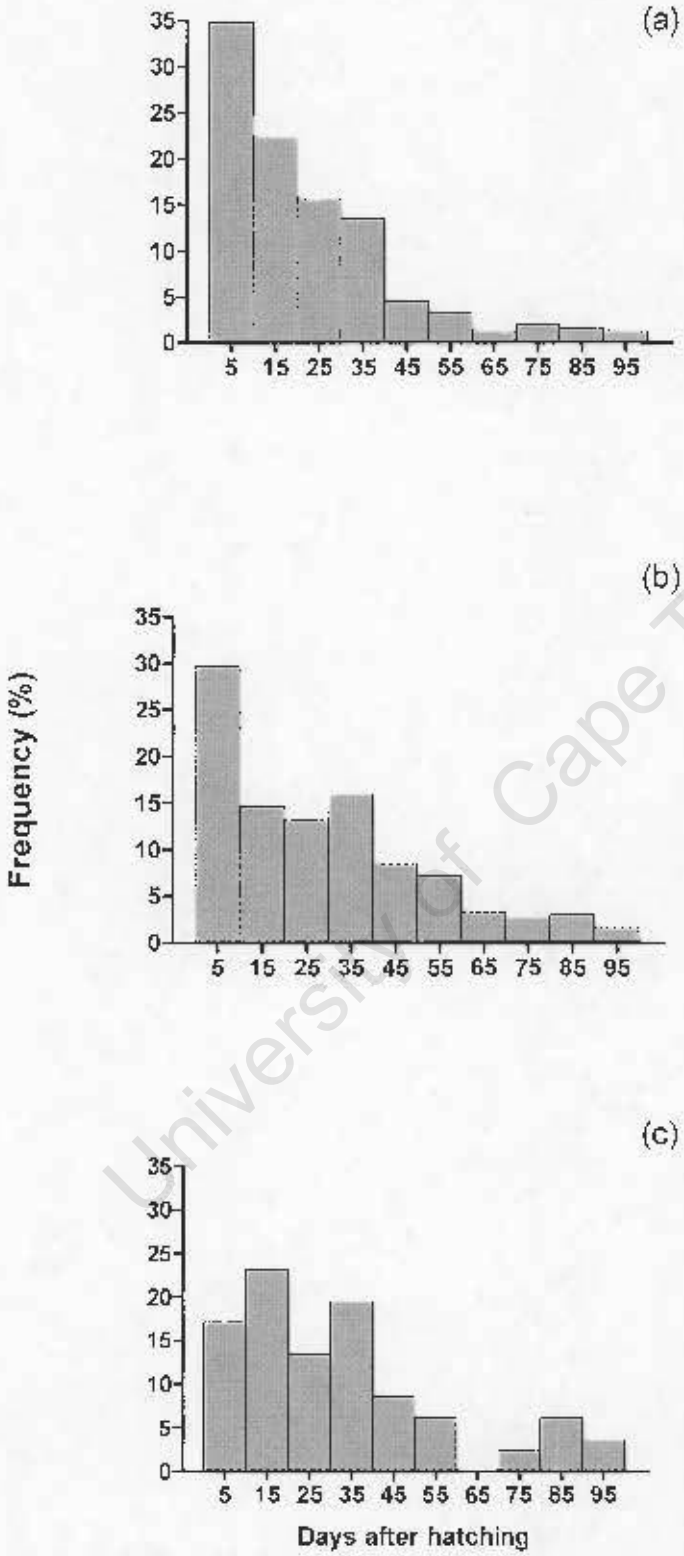

Figure 5.4 Pattern of chick mortality for African Penguins at Dassen Island expressed as the percentage of chicks that died before fledging; (a) Control Nests. (b) *Apollo Sea* Nests. (c) nests with *Apollo Sea* pairs.

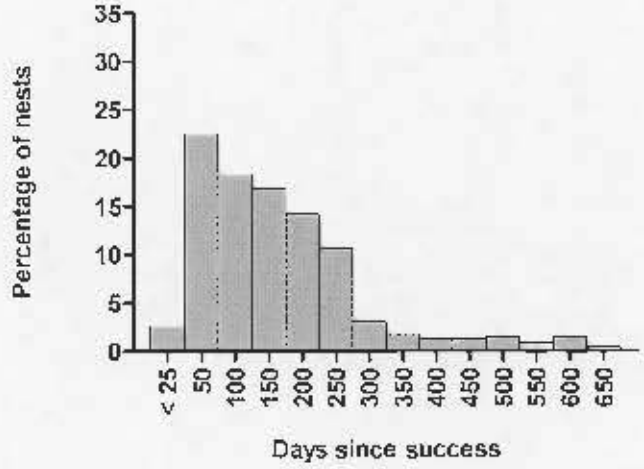

Figure 5.5 Interval between successfully completed or failed breeding attempts and re-laying for banded African Penguins at Dassen Island. Intervals of over 675 days (< 4% of the total) have been excluded from the graphs

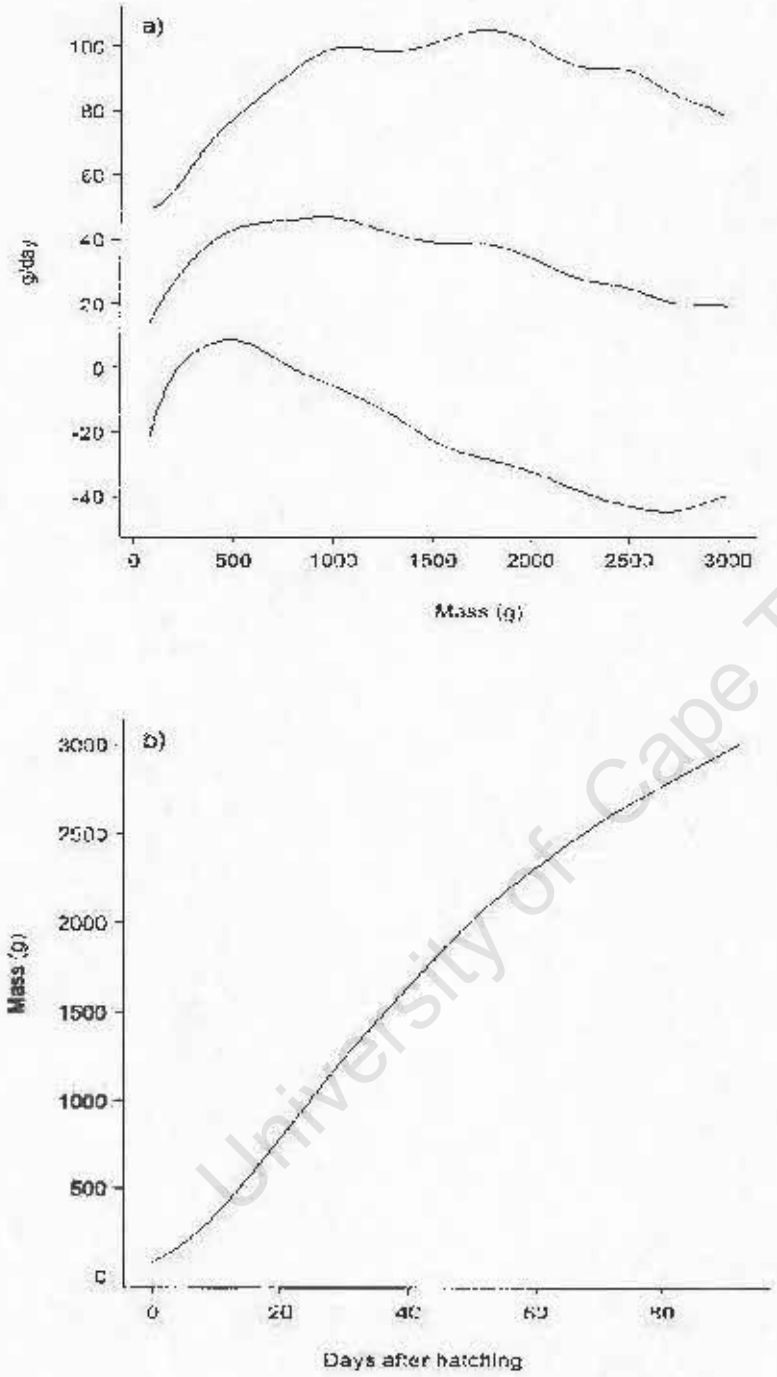

Figure 5.6 a) Growth rate (g/day) to mass plot of African Penguin chicks at Dassen Island. The smoothed curves show the trajectory of the mean, upper and lower 95% confidence intervals (see text for further details); **b)** Growth curve of mass (g) of African Penguin chicks in relation to age in days, transformed from the trajectory of the mean in a).

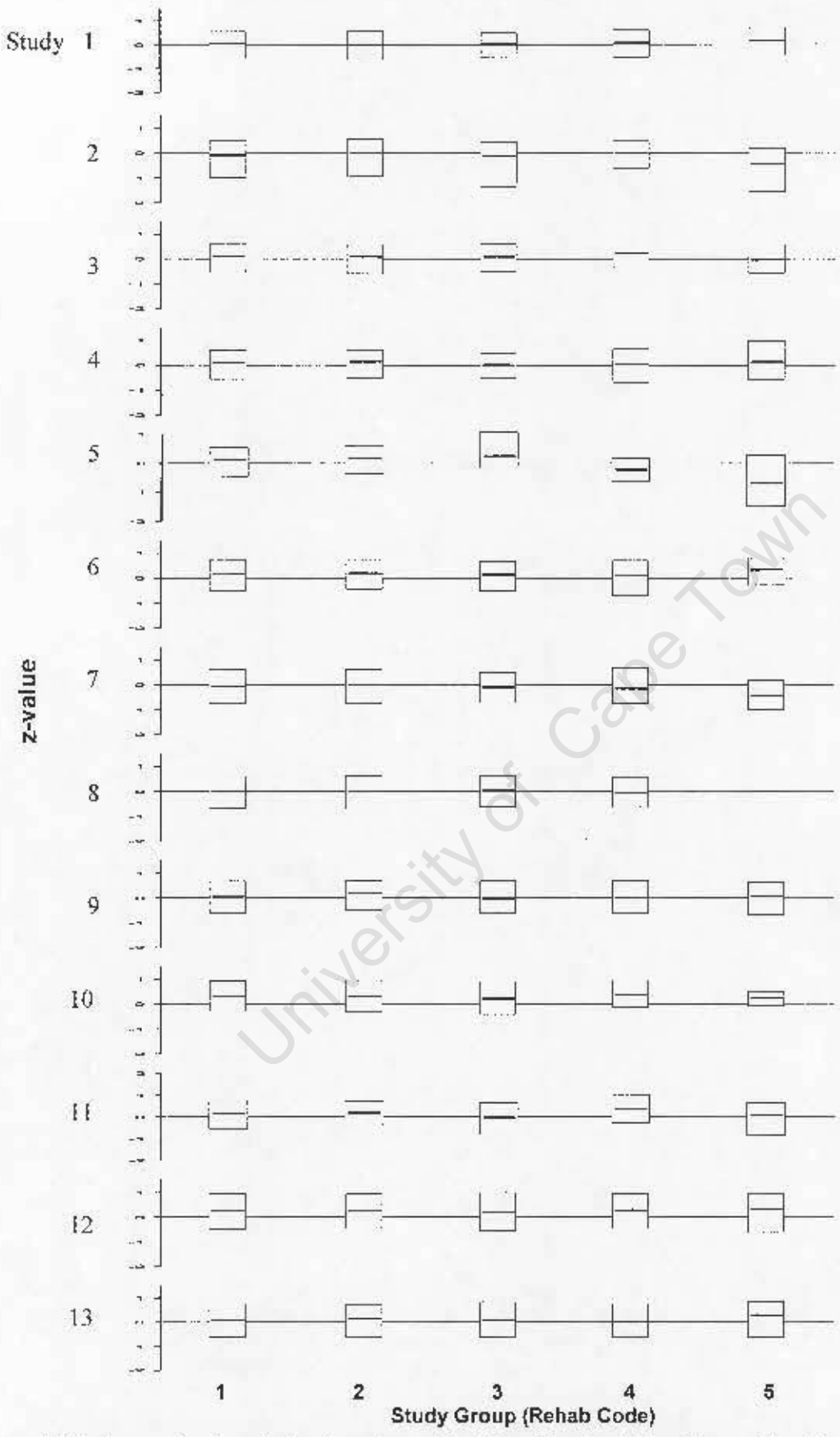

Figure 5.7 Median *z* values (standardized growth rates) for African Penguin chicks at Dassen Island for each study group (Rehab code) in studies 1–13. *z* values are displayed on the y axis, Rehab code on the x axis: 1 = all nests, 2 = control nests, 3 = nests with *Apollo See* females, 4 = *Apollo See* males, 5 = *Apollo See* pair. The solid line across the graph represents the base z score for all studies. Boxes represent the interquartile range of z scores for each study group, and the solid lines within the box, the median *z* values for each study group

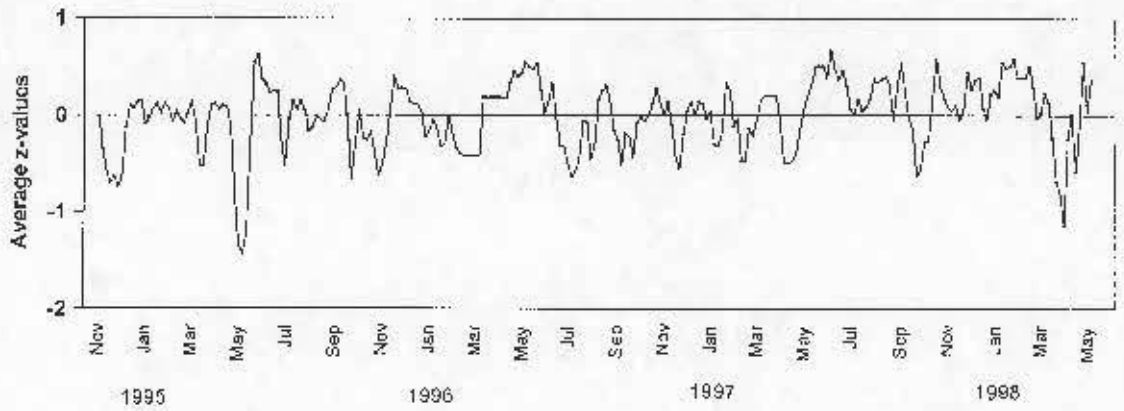

Figure 5.8 Average z-values (standardised growth rates) of all African Penguin chicks per five day interval at Dassen Island, November 1994-May 1998. Positive deviations represent above average growth, and negative deviations below average growth for a specific mass. Every alternate month is displayed on the x-axis

Chapter Six

The impact of the *Treasure* oil spill on African Penguins, especially at Dassen Island: case study of a rescue operation

The impact of the *Treasure* oil spill on African Penguins, especially at Dassen Island: case study of a rescue operation

ABSTRACT

The bulk ore carrier MV *Treasure* sank between Robben and Dassen Island in June 2000. Although releasing less oil than the *Apollo Sea* spill six years earlier, the number of African Penguins *Spheniscus demersus* oiled (approximately 19 000) in the *Treasure* spill was almost double the number oiled in the *Apollo Sea* incident. The majority of oiled penguins were collected from Robben Island. The capture, stabilisation and transport of oiled penguins following the *Treasure* spill were substantially more successful than during the *Apollo Sea* rescue operation. This improvement was due to the implementation of a number of lessons learnt from the shortcomings of the *Apollo Sea* spill, and translated into an increase in the percentage of oiled penguins that were successfully de-oiled and released back to the wild. In addition to the 19 000 oiled penguins that were caught, 19 506 un-oiled birds, 12 345 from Dassen Island, were evacuated to Cape Recife, 800km to the east, to prevent them from becoming contaminated. Three of these birds were fitted with ST-10 satellite transmitters. The evacuated birds returned rapidly to Dassen Island, and many resumed breeding immediately after their return. The restoration success (proportion of birds observed at Dassen Island that were recorded breeding) was substantially greater for evacuated birds than for de-oiled birds. Lightly oiled birds that were released without being cleaned had lower survival rates and were less successfully restored into the breeding population than de-oiled birds, especially if more than 5% of their body was covered in oil. Reproduction exerted a greater cost to de-oiled birds than to evacuated birds. A total of 1 787 orphaned chicks were hand-reared at two separate facilities on the mainland, and were released at Robben and Dassen Islands. The chicks did not necessarily return to the colony at which they were eventually released. The survival rates and restoration success of these two groups of birds differed, probably as a result of the one group being overfed. Despite the death of about 2 000 African Penguins in the *Treasure* spill, and the substantial disturbance that resulted from the rescue operation, the penguin colonies at Robben and Dassen Islands increased by 18% and 26%, respectively, in the year following the spill. This increase was attributed to a significant increase in the biomass of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax* in 2001. The findings in this chapter highlight the importance of preventing oil spills in the first place, and in the event of a large oil spill, the conservation value of evacuating un-oiled penguins to minimise their risk of becoming contaminated.

INTRODUCTION

The African Penguin *Spheniscus demersus* is currently classified as Vulnerable, both regionally and globally (Crawford 2000, Whittington *et al.* 2000, BirdLife International 2004) on the basis of a substantial decline of its population, especially during the 20th century (Crawford *et al.* 1990, 1995). The initial decline in numbers of African Penguins was largely due to direct exploitation by humans, chiefly through harvesting of penguin eggs and the disturbance and habitat alteration associated with scraping of guano (Siegfried & Crawford 1978). These activities have ceased at all penguin colonies in South Africa. More recently, reduced availability of pelagic fish due to competition with commercial fisheries has been responsible for persistent declines (Crawford *et al.* 1990, 2001, Crawford & Dyer 1995). Presently, mortality associated with oil spills is considered to be one of the principal threats to the African Penguin (Whittington *et al.* 2000, Nel *et al.* 2003). The vulnerability of African Penguins to oil contamination is exacerbated by the geographic distribution of their breeding colonies. More than 80% of the population breed within 100km of major shipping harbours (Nel *et al.* 2003).

The incidence of oiling has varied considerably since the closure of the Suez Canal in 1967. Prior to the 1990s, most oiled penguins admitted to the Southern Africa Foundation for the Conservation of Coastal Birds (SANCCOB) were from incidents of unknown origin. In the 1970s and 1980s an average of 0.2% of the population were oiled each year (Adams 1994). The oiling rate increased markedly after 1991; the majority (77%) of African Penguins that were oiled in the period 1968–2002 were from oil spills between 1991 and 2000 (Nel *et al.* 2003). Close to 80% of all penguins oiled in this period were from two major oil spills.

The foundering of the bulk ore carrier *Apollo Sea* in June 1994 caused the worst oiling incident in South Africa up to that time, in terms of the numbers of seabirds (mostly African Penguins) that were contaminated (Underhill *et al.* 1999). The *Apollo Sea* sank about 26km southwest of Dassen Island. Approximately 10 000 African Penguins were oiled, collected and transported to the SANCCOB rehabilitation centre; the majority (8 000 birds) of these were collected from Dassen Island (33°25'S, 18°05'E) (Dehrmann 1994, Erasmus 1995, Underhill *et al.* 1999). Of the 10 000 oiled penguins that were collected, 54% died before they could be released; 53% of these deaths took place

within the initial 48 hours of capture (Williams 1995). Approximately 1 700 birds died during their transport from the island colonies to the rehabilitation centre, probably as a result of excessive handling and poor ventilation, and a further 1 200 birds died during their first 24 hours at the rehabilitation centre (Williams 1995). The large number of deaths in the initial phases of the rescue operation highlighted the lack of preparedness of the conservation authorities for large-scale oil spill events. The survival and restoration success of the 4 076 penguins that were successfully de-oiled and released back into the wild with flipper bands has been well documented (Underhill *et al.* 1999, 2000, Whittington 1999, 2002, Chapters Two, Three and Five).

Six years after the *Apollo Sea* sank, another bulk ore carrier, the MV *Treasure*, sank about 16km north of Robben Island (33°48'S 18°23'E) (Cheney 2000, Crawford *et al.* 2000). The amount of fuel spilt following the sinking of the *Treasure* (1 400 tonnes) (Crawford *et al.* 2000) was less than was spilt following the sinking of the *Apollo Sea* (2 400 tonnes) (Underhill *et al.* 1999). However, the position of the *Treasure* wreck between Dassen and Robben Islands, which supported the largest and third largest colonies of African Penguins at the time (accounting for about 40% of the total population), and the atypical calm weather, which failed to break up and disperse the resulting oil slick, caused the oiling of over 19 000 African Penguins, mostly from Robben and Dassen Islands (Crawford *et al.* 2000). In addition, a further 19 500 un-oiled penguins were evacuated from Robben and Dassen Islands and translocated to Cape Recife (34°02'S, 18°30'E) in the Eastern Cape, to prevent them from becoming oiled (Crawford *et al.* 2000). The number of birds disrupted by the *Treasure* spill was more than four times the number that was oiled following the *Apollo Sea* spill. In terms of impacts on seabirds, the *Treasure* oil spill is the worst oiling incident to affect southern Africa to date.

Following the *Apollo Sea* oil spill a number of recommendations were made to improve the preparedness of authorities to manage large-scale oil spill events (Barrett *et al.* 1995). These recommendations included a post-release monitoring programme to assess the conservation value of de-oiling African Penguins (see Chapters Two, Three and Five). A Conservation Manager was stationed at Dassen Island from 1998. Prior to this a "headman" was based on the island, whose main job was to control human access to the island. A Conservation Management Plan for Dassen Island was developed and

finalised in early 2000 (Wolfaardt 2000). An oil spill contingency plan dealing specifically with the rescue of oil contaminated seabirds at Dassen Island was produced in 1998 (Wolfaardt *et al.* 1998), and is revised annually. In 1999 a seabird stabilisation facility was developed at Dassen Island and equipped with the necessary materials and equipment to respond to a medium-scale oil spill event (i.e. a spill affecting between 30 and 2 000 birds (Wolfaardt *et al.* 1998)). The purpose of this facility is to stabilise injured and oiled seabirds before they are sent to SANCCOB to be de-oiled (Appendix 6.1).

Crawford *et al.* (2000) provided an overview of the *Treasure* oil spill and its initial impacts on penguins, and predicted that the spill would negatively influence breeding activities during 2001, including a reduction in the number of breeding birds at Robben and Dassen Islands. This prediction was based on the death of about 2 000 adult penguins, approximately 3% of the population on these two islands in 2000 (Crawford *et al.* 2000). In addition, there was substantial disturbance to the colonies at Robben and Dassen Islands during the rescue operation and a large proportion of breeding attempts in 2000 was destroyed at either the egg or nestling stage. A more subtle source of reduced breeding success in 2001 was expected to result from birds being separated from their mates during the rescue operation. A large number of un-oiled birds were evacuated from Robben and Dassen Island and translocated to Cape Recife, while oiled birds were held in captivity for variable periods during the de-oiling and treatment process. This was likely to disrupt pair bonds, so that many pairs would be breeding together for the first time in 2001, a condition predicted to reduce breeding success (Crawford *et al.* 2000). The return to Robben Island of three groups of penguins, those that were de-oiled, evacuated and hand-reared, following the *Treasure* spill has been documented by Barham *et al.* (2006) and Barham *et al.* (submitted).

This chapter provides a case study on the rescue operation that followed the *Treasure* spill at Dassen Island in June 2000, and assesses, over the following five years, the efficacy of the operation relative to the rescue of oiled birds after the *Apollo Sea* spill. I investigate the return of de-oiled and evacuated birds to Dassen Island and their restoration into the breeding population, as well as that of hand-reared chicks that were orphaned as a result of the spill. I consider the conservation value of evacuating clean penguins as a management tool in large oil spill events. Overall, I determine the impact

of the *Treasure* oil spill on the breeding population of African Penguins in the years following the spill.

METHODS

Fieldwork protocols

Dassen Island is located approximately 55km north west of Cape Town, 33km south west of Saldanha Bay and 9km west of the coastal town of Yzerfontein, in the Western Cape (Figure 2.1). It is a Provincial Nature Reserve, managed by the Western Cape Nature Conservation Board. The housing and storeroom complex of the Western Cape Nature Conservation Board is located on the northern side of the island, from now on called the base (Figure 6.1). At the time of the *Treasure* spill, conservation staff based on the island comprised a Conservation Manager, an Assistant Manager and a Field Ranger. Immediately following news of the stricken *Treasure*, before it actually sank, the Seabird Rescue Plan for Dassen Island (Wolfaardt *et al.* 1998) was activated. Additional personnel were seconded to Dassen Island from 22 June 2000, one day prior to the sinking of the vessel. From 23 June to 1 July, the coastline of the island was systematically searched for oiled penguins throughout the day, and attempts were made to catch all oiled birds. Catching teams were made up of 5–15 people. The catching teams comprised one or two people in wetsuits who swam around the beach groups of penguins and moved towards them from the seaward side so as to prevent them from fleeing into the water. Other members of the catching team used corral units (lightweight aluminium frames with mesh netting) to "herd" the penguins into a contained group (see Figure 7a of Crawford *et al.* 2000). Once oiled birds were caught, they were placed in well-ventilated plastic crates, and carried to the nearest road access, from where they were transported by vehicle to the island stabilisation facility at the base.

Each penguin admitted to the stabilisation facility was banded with an individually numbered plastic flipper tag. Oiled penguins were placed in temporary pens that were made up using wire mesh corral units with shade cloth. The number of penguins placed in each pen ranged from five to approximately 50, depending on the size of the pen, the main objective being to prevent overcrowding within the pens. Juvenile birds were kept separate from adults to prevent aggressive interactions between the two groups (Ryan

et al. 1987). Weak birds (see Parsons & Underhill (2005) for a definition of "weak") were also separated from the rest of the group. Each oiled bird was treated according to the stabilisation procedure outlined in Appendix 6.1, and detailed records were kept of the treatment history for each individual. The oiled birds were kept at Dassen Island until they could be transported from Dassen Island to Yzerfontein by boat. The birds were transported off the island in cardboard boxes that had been designed for transporting oiled penguins after the *Apollo Sea* spill (see Crawford *et al.* 2000 for details of the dimensions and design). The boxes had been stored flat, and were assembled on the island with packing tape. A team of about 40 people was dedicated to assembling and preparing boxes for the entire duration of the rescue operation. A maximum of three penguins were placed in a box, and juvenile birds were separated from adults. At Yzerfontein the birds were collected by vehicle, and transported the approximately 100km to SANCCOB.

From 25 June, the oil slick started to move northwards from the location where the *Treasure* sank towards Dassen Island; a decision was therefore taken on 26 June to fence off penguin colonies at Dassen Island to prevent penguins from going to sea. Observations at Robben Island had shown that almost all penguins leaving from or returning to the island were becoming oiled because of the proximity of the oil to the island (Crawford *et al.* 2000). At the time of the spill the African Penguin population at Dassen Island was three times the size of the Robben Island population (Wolfaardt *et al.* 2001). By the time the oil spill moved towards Dassen Island, SANCCOB already had thousands of birds in their care (mostly from Robben Island), and were battling to cope with the large number of oiled penguins. The motivation for confining the penguins to the island was to minimise the number becoming oiled.

This was done between 27 June and 1 July 2000, in two ways. Firstly, the wall that surrounds the interior of the island (Figure 6.1) was repaired to serve as a barrier for penguins nesting within its confines, thereby preventing them from entering the sea. The wall was erected in the early 1940s to facilitate the collection of penguin eggs (Rand 1963). After the termination of penguin egg harvesting in 1968 (Shelton *et al.* 1984), the wall fell into a state of disrepair. Sections of the wall had also been actively broken to allow penguins to access the interior of the island (Wolfaardt 2000). The repair work comprised filling in penguin and European Rabbit *Oryctolagus cuniculus* burrows that

had been excavated beneath the wall, digging away sand that had accumulated against the wall, and filling gaps in the wall. Clean penguins on the seaward side of the wall were moved to the inland side of the wall. Secondly, three large penguin colonies outside of the wall were fenced in using plastic mesh fencing and metal droppers (Figure 6.1). Because African Penguins are diurnal foragers (Wilson & Wilson 1995), the fences were opened from about 18h00 each evening to allow un-oiled penguins returning from foraging trips to enter the enclosed areas, thereby maximising the number of penguins held in the fenced areas. The fences were closed before first light the following morning to prevent birds from leaving the enclosed areas.

On 1 July, a helicopter inspection of the sea surrounding Dassen Island revealed a large oil slick encircling the island. A decision was made to begin evacuating un-oiled birds from the island the following day, and to continue for a total of three days. The aim was to relocate as many penguins as possible to Cape Recife so that they could swim back to Dassen Island, allowing sufficient time for the oil to be cleared before their return (Crawford *et al.* 2000). The evacuation operation was limited to three days because there were over a thousand penguins on the island that had already become oiled, and efforts needed to revert to capturing these birds as soon as possible. To facilitate the efficient logistical management of the operation, only clean penguins were caught and removed during the evacuation process. The capture and removal of oiled penguins resumed after the evacuation operation, on 5 July, and continued until 28 July.

The capture of clean penguins began at colonies that had been fenced in for longest. Penguins that were standing outside of burrows in the colony were herded by a group of catchers into a corral unit. Large groups of penguins herded into the corral unit were separated into smaller groups to avoid overcrowding and stress to the birds. All oiled penguins and juveniles were immediately released, so that only clean adult penguins were evacuated. In the largest colonies, two or three "herding sweeps" were conducted. After the majority of birds outside of burrows had been collected, the capture team worked systematically through the burrows of the colony, removing all clean adult birds, marking each nest by scraping a cross in the ground to show that the birds had been removed. Two or three record keepers were stationed at the capture sites to record the flipper-band numbers of penguins that were caught and boxed. The number of people working in the colonies was limited to reduce the incidence of collapsing burrows.

Penguins were first packed into ventilated plastic crates (10 penguins to a crate), then taken by foot to outside of the colony area, where they were packed into the penguin transportation boxes. Penguin boxes were transported to the capture site, either directly by vehicle, or if this was not possible, by vehicle and then by foot. Two light delivery vehicles (bakkies) were used, each towing a trailer. Birds were not herded into the corral units, or collected from burrows, before sufficient boxes were available at the capture point. Five penguins were placed in a box, and the boxes were then closed and placed on a bakkie and trailer. When each bakkie and trailer was full it returned to the base. The bakkies operated in such a manner so as to ensure that when the one bakkie departed from the capture point the other one arrived. This helped prevent disruptions to the operation, and minimised the amount of time that birds were held in the corral units.

Upon arrival at the base, the bakkie and trailer were offloaded by a separate team. The boxes (and penguins) were counted and placed in the shade until there were sufficient boxes to be transported to Yzerfontein. A record-keeper was stationed at the base and was devoted entirely to keeping accurate records of the numbers of boxes (and penguins) which left the island. On the first day of the evacuation operation (2 July), the penguins were transported from Dassen Island to Yzerfontein by boats and a Sikorski helicopter. On the second and third day of the operation, only the helicopter was used because it was found to be a more effective means of maximising the number of penguins transported to Yzerfontein.

Once the boxes of penguins arrived at Yzerfontein, a separate team unloaded the boxes from the boats or helicopter, and re-packed the penguins so that there were three birds to a box. On the island, penguins were packed five to a box to maximise the number of penguins that could be sent off the island in the limited time that was available. Due to the relatively long truck trip to Port Elizabeth, the penguins were re-packed three to a box to prevent problems with overcrowding and ventilation. Tiered sheep trucks were used to transport the penguins from Yzerfontein to Port Elizabeth. Once the trucks arrived at Cape Recife, the boxes were offloaded and the penguins released immediately.

On the final day of the penguin evacuation (4 July), a team began collecting chicks that had become orphaned as a result of their parents having been sent off the island. The

chick collecting activities were initially focused in the areas where adults had been evacuated, and at a later stage moved into areas where large numbers of oiled penguins had been caught. The collection of abandoned chicks took place from 4 July until 14 July. All chicks were sent to the satellite rehabilitation centre that had been set up at Salt River, in Cape Town. Upon arrival, the chicks were screened by veterinary personnel before being sent to one of the chick-rearing centres. Chick rearing centres were established at SANCCOB and its satellite centre in Salt River, and at a private rehabilitation centre in Melkbosstrand (33°43'S 18°26'E), called Monty's. Chicks removed from Dassen and Robben Islands were not kept separate. The natal island of the chicks at the different chick rearing centres was therefore not known. Chicks that were hand-reared at Monty's were later released on Dassen Island; chicks hand-reared at SANCCOB and its satellite station, were released on Robben Island.

On 5 July the fences were removed, and the exclusion wall surrounding the interior of the island was re-opened so that penguins remaining within these confines could enter the sea to feed. Oil that washed ashore on Dassen Island was cleaned using peat-based absorbents (Crawford *et al.* 2000) from 5 July until 15 July.

Flipper-banding penguins

In order to monitor the efficacy of the translocation intervention, a total of 969 penguins from within the fenced off areas, were fitted with flipper-bands on 1 July. Many of the penguins that became oiled as a result of the *Treasure* spill had only small and superficial patches of oil on their plumage. Those that were lightly and superficially oiled were treated as clean birds, and were not de-oiled. On 8 July, 255 penguins that were lightly oiled were caught at Whale Bay and House Bay. For each bird, the extent of the oiling was classified into one of the following percentage categories: <5%, 5%, 10%, 15% and 20%, which represented the percentage of body covered in oil. Whether the contamination was superficial or had reached the skin of the penguin was also indicated. Subsequent re-sightings of these penguins were made from August 2000 until March 2005, and for adults the re-sighting probabilities in each oiling category were analysed using a generalized linear model. The un-oiled evacuated penguins (all adults) which were flipper-banded were used as a control baseline against which to compare the oiling categories. These birds were banded at approximately the same time and in the same areas as the experimental birds.

Two of the penguins that were translocated from Dassen Island to Cape Recife, and one of the penguins translocated from Robben Island, were fitted with ST-10 satellite transmitters (Crawford *et al.* 2000). The instruments were fitted to the back of the penguins by means of Velcro©. The Robben Island penguin (named Peter) was released at Cape Recife on 30 June. The Dassen Island birds (Pamela and Percy) were released at Cape Recife on 3 and 5 July, respectively. Peter's device transmitted on a cycle of 8 hours on and 24 hours off; the transmission cycle for Percy and Pamela's devices were eight hours on 16 hours off and 12 hours on, 12 hours off, respectively (Crawford *et al.* 2000). The three penguins fitted with ST-10 devices were all in adult plumage. The sexes of the birds were assigned visually, using the relative sizes of their culmens (Cooper 1972). The return trips of the three penguins were monitored using co-ordinates downloaded to the Argos Services Centre in Toulouse, France (Crawford *et al.* 2000). Movement data were plotted using ARCVIEW GIS Version 3.2a (Environmental Systems Research Institute Inc., U.S.A.).

An intensive programme to re-sight flipper-banded penguins at Dassen Island was instituted in September 1994, after the *Apollo Sea* oil spill, and continued until March 2005. Details of the collection of re-sighting and recovery data are provided in Chapter Two. The bird ringing and re-sighting database curated by the South African Bird Ringing Unit (SAFRING) was checked for any records of "Dassen Island" birds that had been seen elsewhere, either dead or alive. These sightings were incorporated into the Dassen Island database so that they could be included in the analyses. Twenty of the flipper-banded penguins that were translocated were weighed upon their return to Dassen Island with a Salter® spring balance to an accuracy of 25g.

Counts of active nest sites of African Penguins have been conducted annually at Dassen Island and most other South African colonies since the late 1980s. Details of the methodology used are provided in Chapter Four.

Capture-mark-recapture (CMR) models

I used multi-state capture-mark recapture models, which separate survival from recapture rates, to estimate the survival of three groups of birds that were re-sighted at Dassen Island: 1) De-oiled adult birds from the *Treasure* spill; 2) Un-oiled adults that were evacuated; and 3) Hand-reared chicks that were orphaned as a result of the spill. I only included the hand-reared chicks that were released on Robben Island (i.e. hand-reared at SANCCOB) because there were insufficient data to estimate survival for the hand-reared chicks released on Dassen Island (i.e. those hand-reared at Monty's). As in Chapter Two, I defined three states that penguins could assume: 1) nonbreeders (n); 2) breeders (b); and secondary nonbreeders (s) (see Chapter Two and Figure 2.3). A bird was defined as a breeder if it was recorded with eggs or chicks; nonbreeders were birds observed at Dassen Island, but not with eggs and/or chicks. A secondary nonbreeder was a bird that was observed in a particular year as a nonbreeder, but had previously been recorded breeding (subsequent to the *Treasure* oil spill).The models were also used to estimate the probability of an individual making the transition from the nonbreeder state to the breeder state, and for a breeder to become a secondary nonbreeder for the three groups of birds.

I anticipated the re-sighting data to contain transients. Transients are birds that were sighted once, but never again, and likely comprise "visiting", rather than resident birds. A mixture of transient and resident birds causes survival to be underestimated (Pradel *et al.* 1997). I therefore accounted for the effect of transients by allowing survival to be lower during the intervals following the initial sighting of these birds. I only report survival rate for resident birds. I did not account for transients amongst breeders because once birds initiate breeding activities at a colony, they almost always remain resident there (Randall *et al.* 1987, Crawford 1998, Whittington *et al.* 2005a). Details of the re-sighting methodology were provided in Chapter Two.

I restricted the analysis to all birds that were re-sighted at Dassen Island after the *Treasure* oil spill. The starting point was therefore the initial sighting of an individual at Dassen Island, rather than the banding and release of the individual from the rehabilitation centre(s), or Cape Recife, in the case of the evacuated birds. Recapture periods were not calendar years, but were set to start in March and end in February of the following year, except for 2000, which started in July 2000 (the first month after the

Treasure spill) and ended in February 2001. The February to March recapture period was selected so as to coincide with the end of the peak moult period (February) for penguins at Dassen Island (Chapter Three). Details of the re-sighting methodology were provided in Chapter Two. Re-sighting data were collected from July 2000 to March 2005. This allowed survival to be estimated annually for 2001–02, 2002–03 and 2003–04 and over an eight month period for the 2000–01 interval.

The most general model contained transient and time effects on all three groups for survival, except that breeder survival was constant for the orphaned chicks, which were few in number (Model 3, Table 6.7). In this model, recapture rates were variable over time, except for breeders, where it was constant. The probability of transition from nonbreeder to breeder state (Ψ_{nb}) varied among groups and years, and the probability of transition from breeder to secondary nonbreeder state (Ψ_{bs}) and secondary nonbreeder to breeder state (Ψ_{sb}) varied among groups. I assessed the goodness of fit for this model using a procedure based on Monte Carlo simulation, called the median *c*-hat approach in programme MARK 4.3 (White & Burnham 1999). The test showed that there was slight overdispersion (estimated *c*-hat = 1.23, SE = 0.03). I used this estimate as a variance inflation factor and adjusted the standard errors and confidence intervals accordingly.

All other models were simplified versions of this general model. Model 4 had constant Ψ_{bs} and Ψ_{sb} (Table 6.7). Model 2 kept the recapture rate of nonbreeders constant over time. Model 1 further ignored the possibility of transients among the evacuated group. Models 5 and 6 were like Model 1, except they treated de-oiled birds and evacuees equal in terms of survival (Model 5) and Ψ_{nb}(Model 6). I based model selection on the sample-size adjusted Akaike's Information Criterion (AICc, Burnham & Anderson 2002).

RESULTS

Numbers of birds caught and rescued

The first oiled penguins were observed ashore at Dassen Island on 24 June, one day after the *Treasure* sank. From 25 June to 28 July a total of 3 530 oiled penguins were collected at Dassen Island (Table 6.1). Of the birds caught on the island, 14 died before

being sent to SANCCOB, 11 birds in adult plumage and three juveniles. The majority (78%) of the oiled birds sent to SANCCOB were in adult plumage; the remainder comprised juvenile birds (21%) and four feathered chicks (Table 6.1). Sixty percent of the total number of oiled penguins sent off the island had been caught by 2 July, when the evacuation of clean penguins began. By 8 July, when the shoreline of the island was largely clear of oil (Crawford *et al.* 2000), 95% of the oiled penguins had been sent off the island (Table 6.1). Of the oiled birds collected at Dassen Island, 52 were flipper-banded prior to the spill, 19 of which had been oiled and treated by SANCCOB previously. In total, 14 825 oiled African Penguins were collected at Robben Island (Crawford *et al.* 2000).

From 2 to 4 July a total of 12 345 un-oiled adult African Penguins were caught at Dassen Island (Table 6.1). Pamela was released at Cape Recife on 3 July 2000, and Percy was released there on 5 July. Of the un-oiled birds evacuated from Dassen Island, 1 019 were flipper-banded. An additional 7 161 un-oiled penguins were translocated from Robben Island to Cape Recife, of which 2 232 were flipper-banded (Crawford *et al.* 2000, Barham *et al.* 2006). Peter was released from Cape Recife on 30 June 2000 (Barham *et al.* 2006). All birds evacuated from Dassen Island were transported in three-tiered trucks normally used to transport sheep, whereas birds evacuated from Robben Island were transported in closed trucks. The Robben Island birds were held for 24–48 hours at the Marine and Coastal Management research aquarium in Sea Point (33°54'S, 18°23'E) before they were transported to Cape Recife (Crawford *et al.* 2000).

From 4 to 14 July, 707 orphaned chicks were collected at Dassen Island and sent to the Salt River satellite rehabilitation centre (Table 6.1). Approximately 2 600 orphaned chicks were collected from Robben Island for captive rearing (Crawford *et al.* 2000). The 255 lightly oiled birds that were flipper-banded and released again at Dassen Island on 8 July without being de-oiled comprised 181 birds in adult plumage and 74 juveniles (Table 6.2). The majority (79%) of these birds had five percent or less of the underside of their bodies covered by oil (Table 6.2).

Numbers of birds released

A total of 17 287 de-oiled birds, 91% of the oiled birds that were caught after the *Treasure* spill, were successfully returned to the wild (Crawford *et al.* 2000). The majority

were released between 19 July and 30 August 2000 at Milnerton beach (33°51'S, 18°29'E) and were wearing steel flipper bands. It was not known at which island each bird had been collected, and therefore how many of the oiled birds collected at Dassen Island were amongst the 17 287 de-oiled birds that were successfully released.

Of the 19 506 evacuated birds trucked to Cape Recife, 241 died before being released, or at the release site (Crawford *et al.* 2000). Seventeen of these birds had flipper bands; 16 had been evacuated from Robben Island, and one from Dassen Island. These mortalities represent 2.2% and 1.4% of the total number of flipper-banded birds evacuated from Robben Island and Dassen Island, respectively. Applying these percentages to the total number of birds released from each island over represents the total number of mortalities by about 37%, suggesting that a greater proportion of flipper-banded birds died during the evacuation process than unbanded birds.

From 29 July to 6 November 2000, a total of 732 chicks hand-reared at Monty's rehabilitation centre, were released on Dassen Island. An additional 1 055 hand-reared chicks from the SANCCOB facilities were released on Robben Island (Barham *et al.* submitted). Hand-reared chicks were released with flipper bands.

Re-sightings of de-oiled birds

From July 2000 to March 2005, 6 721 re-sightings of 2 818 de-oiled adult birds were made at Dassen Island. It is not known what proportion of these were among the 3 530 originally collected, as oiled birds, from Dassen Island. Twenty-eight percent of the de-oiled adults re-sighted at Dassen Island were also observed at Robben Island during the study period. Of the de-oiled adults re-sighted at Dassen Island, 55% had been re-sighted by the end of August 2001, approximately one year after their release; 80% and 92% had been re-sighted by the end of August 2002 and August 2003, respectively (Table 6.3, Figure 6.2a).

Of the de-oiled adult birds that were re-sighted at Dassen Island, 841 (30%) had been recorded breeding by March 2005 (Table 6.3). By the end of August 2001 (i.e. within one year of their release), 16% of the de-oiled birds re-sighted at Dassen Island had been recorded breeding (Table 6.3, Figure 6.2a). This represents 29% of the 841 de-oiled birds recorded as breeders during the study period. The proportion of re-sighted de-oiled

birds that were recorded breeding each year increased from 3.8% in 2000 to between 34% and 37% from 2002–2005 (Table 6.4). The mean number of years in which de-oiled birds were recorded breeding during the study period was 1.37 (SD = 0.77 years, n = 841 birds).

A total of 274 de-oiled penguins released in juvenile plumage were observed at Dassen Island between July 2000 and March 2005, 60 of which were also re-sighted at Robben Island. Of the de-oiled juvenile birds re-sighted at Dassen Island, 42 (15.3%) were recorded breeding.

Re-sightings of lightly oiled birds

Of the 181 lightly oiled adult birds that were banded and released without being de-oiled on 8 July 2000 at Dassen Island, 104 (59%) were observed at Dassen Island between September 2000 and March 2005. None of the birds that were deeply oiled were re-sighted. In total 67% of the birds that were less than 5% contaminated were re-sighted (Figure 6.3). The proportion of lightly oiled birds re-sighted decreased as the extent of contamination increased, from 55% (for birds that were 5% contaminated) to 0% (for birds that were 20% contaminated) (Figure 6.3). This outcome was evaluated for adults using a generalized linear model. Using the un-oiled evacuated birds as controls, the degree of oiling was entered into the model as a categorical variable. The modelled re-sighting probability for penguins with less than 5% oiling was not significantly different from that of un-oiled birds (P=0.114). However, higher levels of oiling were associated with significantly lower re-sighting probabilities than that of un-oiled birds (5% oiling, P=0.001; 10%, P=0.005; 15% or more, P=0.057, but the sample size for this category was only four). The proportion of re-sighted birds that were recorded breeding decreased with the degree of oiling, from 28% for birds less than 5% contaminated, to 25% for birds with 5% contamination, and 6% for birds that were 10% oiled. No birds that were greater than 10% oiled were recorded breeding (Figure 6.3). The results of the generalized linear model for flipper-banded adults resuming breeding indicated that even for penguins which were less than 5% oiled, the probability of resuming breeding after capture was significantly lower than for un-oiled birds (P<0.001). The remaining categories also showed significantly reduced probabilities (all P<0.001). No lightly oiled adults were recorded breeding in 2000 (Table 6.4). In 2001, 10% of the lightly oiled

adults re-sighted were recorded breeding; from 2002–2005, this proportion fluctuated between 30% (in 2003) and 38% (in 2002) (Table 6.4).

Fifty percent of the lightly oiled juveniles were re-sighted during the study period (Table 6.5). Larger proportions of birds with oil contamination of 5% or less were re-sighted than those with greater levels of oil contamination; no juveniles with greater than 10% contamination were re-sighted (Table 6.5). Four lightly oiled juveniles, all less than 10% contaminated, were recorded breeding by the end of March 2005 (Table 6.5).

Re-sightings of evacuated birds

In total, 766 (68%) of the flipper-banded birds evacuated from Dassen Island were re-sighted there between July 2000 (after their release) and March 2005 (Table 6.3). Evacuated birds were re-sighted at Dassen Island from 14 July 2000. The shortest interval between translocation and first sighting at the island was 11 days. The median interval between release and first sighting was 101 days (five number summary: 11, 29, 101, 291, 1627). By the end of July 2000 (i.e. within a month of the evacuation), 194 evacuees had been re-sighted. This figure represents 19% of the total number of evacuees that were released with flipper-bands, and 25% of the flipper-banded evacuees that were re-sighted during the study period. By the end of August 2001, 84% of the re-sighted birds had been recorded (Table 6.3, Figure 6.2). The mean mass of evacuees first re-sighted between 14 July 2000 and 19 July 2000 was 3.36kg (SD = 0.42kg, n = 20 birds) This mean is higher than the mean masses of both male and female African Penguins, given by Hockey *et al.* (2005) as 3.31 and 2.96, respectively. Twelve (1.2%) of the 1 019 flipper-banded birds that were evacuated from Dassen Island were observed at Robben Island during the study period; all were also re-sighted at Dassen Island.

In total 521 (68%) of the re-sighted evacuees were recorded breeding during the study period (Table 6.3). Thirteen were recorded breeding within a month of their evacuation from Dassen Island. During the first year following the evacuation, 404 evacuees had been recorded breeding (Table 6.3). This figure represents 63% of the total number of evacuees re-sighted at Dassen Island, and 78% of the total number of evacuees that were recorded breeding (Figure 6.2b). The pattern of cumulative re-sightings over time indicates a more rapid return of evacuees to Dassen Island compared with de-oiled

birds, and a substantially faster rate of restoration into the breeding population (Figures 6.2a,b). For example, by August 2002 (two years after the event), 2 248 de-oiled penguins had been re-sighted and of these 590 (26%) had been recorded breeding; for evacuated penguins these values were 734 and 500 (68%), respectively; this difference is significant (χ^2 = 418.4, df = 1, P<0.001). The proportion of re-sighted evacuees breeding each year was lowest in 2000 (47%), and highest in 2002 (70.2%), and was on average double the proportion of de-oiled and lightly oiled birds recorded breeding each year (Table 6.4). The mean number of years in which evacuees were recorded breeding was 2.12 (SD = 1.24 years, n = 521 birds), significantly greater than the frequency of breeding for de-oiled birds (t = 13.97, df = 1360, P < 0.001).

Of the 2 232 flipper-banded penguins evacuated from Robben Island, 677 (30%) were re-sighted at Dassen Island. Sixty-two of these birds were also observed at Robben Island and were probably transient visitors to Dassen Island when they were observed there. The remaining 615 birds were never re-sighted at Robben Island after their evacuation. A total of 408 of the Robben Island evacuees were observed breeding at Dassen Island, equivalent to 60% of the total number of Robben Island evacuees observed at Dassen Island, and 66% of the birds that were observed only at Dassen Island. In the first year following the evacuation 228 of the Robben Island evacuees were recorded breeding at Dassen Island, 56% of the total that were recorded breeding during the study period.

Re-sightings of hand-reared chicks

Between January 2001 and March 2005, 361 (20.2%) of the 1 787 hand-reared chicks released with flipper bands were re-sighted at Dassen Island (Table 6.6). A significantly greater proportion of the birds released on Robben Island (27%), compared with those released on Dassen Island (11%), were re-sighted at Dassen Island (X^2 = 43.3, df = 1, P < 0.001; Table 6.6). In total 82 of the hand-reared chicks released on Dassen Island were observed between 2001 and 2006 at Robben Island (Barham *et al.* submitted), 10 of which were also observed at Dassen Island. The majority (71%) of the 287 hand-reared chicks re-sighted at Robben Island were birds that were released on Robben Island (Barham *et al.* submitted). Fifty of the 205 orphans that were released on Robben Island and later re-sighted there were also observed at Dassen Island. The proportions of hand-reared chicks re-sighted at Dassen Island that were recorded breeding there

was 9.9% of the birds released at Dassen Island and 9.3% of those released at Robben Island (Table 6.6).

Return of Peter, Pamela and Percy

The three evacuated penguins equipped with satellite transmitters returned to their colonies between 18 and 25 July 2000, within three weeks of their release from Cape Recife (Figures 6.4a,b,c). The return journeys of Peter, Percy and Pamela took approximately 18, 15 and 20 days, respectively. After passing Cape St. Francis, south of the town of Humansdorp, Peter and Percy remained relatively close to the coastline (within 20km of the coast) until Plettenberg Bay (Figures 6.4a,c), whereas Pamela travelled farther away from the coast, and was approximately 45km offshore when passing Plettenberg Bay (Figure 6.4b). Both Peter and Percy moved farther offshore after passing Plettenberg Bay, and remained away from the coastline until just east of Cape Agulhas (34°50'S, 20°02'E). Pamela continued to travel relatively far from the coast (between 25km and 65km offshore) until 15 July, when she moved closer inshore near Stilbaai (34°23'S, 21°25'E). Percy and Pamela followed similar routes from Cape Agulhas, travelling across the entrance of False Bay and moving west of Robben Island, before making landfall at Dassen Island (Figures 6.4b,c). Peter travelled farther offshore around Cape Agulhas than the other two birds, but followed a similar route thereafter until it made landfall at Robben Island on 18 July (Figure 6.4a).

CMR results

Model selection favoured a model with constant recapture rates for nonbreeders and breeders, time and group effects on survival, together with transient effects for de-oiled adults and orphaned chicks (Model 1, Table 6.7). Model 1 was therefore used to estimate the survival and breeding parameters. Model 1 also indicated variation in the transition from nonbreeder to breeder (Ψ_{nb}) between groups and years, and variation between groups in the transition from breeder to secondary nonbreeder (Ψ_{bs}), and from secondary nonbreeder to breeder (Ψ_{sb}) (Table 6.7). The improved fit of Model 1 to the data compared with Models 5 and 6, in which de-oiled birds and evacuees were treated equal in terms of survival and Ψ_{nb}, indicates that survival and the probability of transition from nonbreeder to breeder differed between these two groups (Table 6.7, ΔAICc = 19.97 and 56.68 for survival and probability of breeding, respectively).

The mean survival of de-oiled breeders remained lower than evacuated breeders throughout the study, ranging from 7% lower for the period 2000-2001, to 17% lower for the periods 2001–02 and 2002–03 (Figure 6.5). The survival estimates for the first interval (2000–01) are for an eight month period, and so would be expected to be slightly higher than the annual survival estimates in the other periods (Figure 6.5).The mean survival of de-oiled and evacuated nonbreeders varied similarly throughout the study. For both groups, the mean survival rates declined in the period 2002–2003, before increasing again in 2003–2004 (Figure 6.6). For evacuated birds, the reduction in the survival rate in 2002—03 and the large confidence intervals in 2003–04 (Figure 6.6) probably reflect the reduced size of the nonbreeding population (the models predict that by the end of the 2002 interval, 69% of the surviving evacuees had resumed breeding, Figure 6.6).

In the first year following the *Treasure* spill (the period 2000–01), the model predicted that 44% of the evacuated birds resumed breeding, compared with 12% of the de-oiled birds (Figure 6.7). These figures are lower than those obtained from the re-sighting data alone, because the CMR models quantify the probability of a bird making the transition from nonbreeder to breeder state, and only include breeding records that are preceded by a "nonbreeding" sighting. The proportions of evacuated and de-oiled birds that resumed breeding in 2001–02 and each subsequent period were similar (Figure 6.7). Consequently, the overall proportion of re-sighted evacuees that resumed breeding was substantially greater than for de-oiled birds.

The improved fit of Model 3 over Model 4 (ΔAICc = 13.62, Table 6.7), in which the modelled transition from breeder to secondary nonbreeder (Ψ_{bs}) was kept constant, shows that this transition differed between groups. De-oiled adults stopped breeding at a higher rate (mean = 0.44, SE = 0.03) than evacuated birds (mean = 0.30, SE = 0.02) over the course of the study.

The estimated annual survival rates for hand-reared orphans released at Robben Island and re-sighted at Dassen Island was 0.60 for the period 2001-02; it decreased to 0.41 in 2002–03, and increased again to 0.79 in the period 2003–04 (Figure 6.8). During the first year following the spill (2000–01), residents could not be separated from transients, and so I was unable to estimate accurately survival for this period. No orphaned chicks were

recorded breeding in the first two years after the spill. The model suggests that 8.5% of the surviving orphans initiated breeding from 2002–2003 (95% confidence interval: 3.4% to 19%), and an additional 20.4% from 2003–2004 (95% confidence interval: 10.4% to 36.4%).

Population trends following the *Treasure* spill

Census information from all South African penguin colonies indicated that the year following the *Treasure* spill (2001) was a good breeding year for African Penguins, with an overall year-on-year increase in the number of breeding pairs of 18.8% (Table 6.8). Based on counts of active nest sites, the number of breeding pairs at Dassen Island increased from 17 042 counted in April 2000 to 21 409 in April 2001, an increase of 25.6%. At Robben Island, where most oiled penguins were collected in 2000 (Crawford *et al.* 2000), the number of breeding pairs in 2001 showed an increase of 17.8% on the count in 2000. All of the penguin colonies on islands in Saldanha Bay (Marcus, Malgas, Jutten and Vondeling Islands) had larger numbers of breeding pairs in 2001 compared with 2000. The number of penguin breeding pairs counted at Bird Island in Algoa Bay in 2001 represented the largest number ever recorded there (Table 6.8, MCM, unpubl. data).

DISCUSSION

Rescue and de-oiling success

The impact of an oil spill is influenced more by the location of the spill and the prevailing conditions than the quantity of oil that is spilt (Morant *et al.* 1981, Whittington 2002, 2003). The *Apollo Sea* sank southwest of Dassen Island in June 1994, releasing approximately 2 400 tonnes of oil, and contaminating about 10 000 African Penguins (Erasmus 1995, Underhill *et al.* 1999). Six years later the *Treasure* sank between Dassen and Robben Islands, which at the time supported the largest and third largest colonies of African Penguins, respectively (Cheney 2000, Crawford *et al.* 2000, Kuyper & Williams 2004). Although the oil released from the *Treasure* wreck was 58% (1 400 tonnes) of the amount spilt by the *Apollo Sea*, it resulted in the contamination of 90% more penguins (19 000), and prompted the evacuation and relocation of an additional

19 500 penguins (Crawford *et al.* 2000). Thus the *Treasure* spill, roughly half the size of the *Apollo Sea* spill, impacted nearly four times as many penguins.

Despite this fourfold increase in the number of birds that were handled during the *Treasure* oil spill, the mortality rate of penguins in the initial stages of the rescue operation was substantially lower than was the case during the *Apollo Sea* spill. In the *Apollo Sea* spill, 53% of all the approximately 5 200 deaths occurred at the beginning of the rescue phase, within the initial 48 hours of removal from their colonies (Williams 1995). The majority of these birds died while being transported to SANCCOB, or within 24 hours of arriving there, probably as a result of excessive handling and poor treatment during the capture and transportation process (leading to increased stress levels), and inadequate ventilation while in transit (Williams 1995). Of the 15 875 penguins that were captured on Dassen Island following the *Treasure* spill, only 14 (0.09%) died before being transported off the island. By 18 August 2000, a total of about 2 000 adult and juvenile penguins had died, 11% of the approximately 19 000 that were oiled (Crawford *et al.* 2000). The greater success in the early stages of the *Treasure* spill translated into a higher release rate. Approximately 90% of the oiled penguins collected after the *Treasure* oil spill were successfully released after de-oiling (Crawford *et al.* 2000), compared with 46% following the *Apollo Sea*, equivalent to 75% of the birds that survived their first 24 hours in captivity (Williams 1995, Nel *et al.* 2003).

The improved success in the capture phase of the rescue operation and in the final release of de-oiled birds was due largely to the implementation of measures to remedy the shortcomings raised by Williams (1995) regarding the capture phases on Dassen Island after the *Apollo Sea* spill: lack of suitable penguin transport containers, which resulted in large numbers of deaths during transport, lack of, or inefficient, communication between the island and the mainland, and a severe shortage of trained and motivated personnel to assist with the rescue operation. Firstly, SANCCOB designed a well-ventilated penguin transport box, with explicit guidelines for its use (Crawford *et al.* 2000). Secondly, the introduction of the cellular phone, and its mainstream use after 1994 facilitated vastly improved communication during the *Treasure* rescue operation, both on the islands, and between the islands and the mainland. Thirdly, there was a better level of preparedness at SANCCOB and the islands for an oil spill event. This was especially the case at Dassen Island, where a

dedicated conservation manager was deployed permanently after the *Apollo Sea* spill, and whose first tasks were to formulate a management plan, which included an oil spill contingency component, and to establish a properly equipped seabird stabilisation facility on the island. These interventions helped ensure that the rescue operation was conducted in an efficient and informed manner. Most oiled birds collected at Dassen Island received stabilisation treatment before they were transferred to SANCCOB, which likely contributed towards minimising mortalities, both in the early stages of the operation, and through the entire de-oiling process. Had the *Apollo Sea* spill not occurred in 1994, the rescue operation and rehabilitation of penguins following the *Treasure* spill would almost certainly have been far less successful.

The successful implementation of lessons learnt from the *Apollo Sea* was facilitated by the short interval (six years) between the two spills. The institutional memory and expertise that was built during the *Apollo Sea* spill was still largely in place at the time of the *Treasure* spill, and with better systems in place, this expertise was put to far better use than during the *Apollo Sea* spill. This collective experience also facilitated crisp decision-taking after short but in-depth expert conferences that formed part of the daily planning during the rescue operation. Two key decisions were taken by this expert group: to confine penguins to the island, and to evacuate them to Cape Recife. With the benefit of hindsight, both interventions improved the success rate of the rescue operation (see below).

De-oiling versus Evacuation

Prior to the *Treasure* spill, the main focus of South African seabird rescue operations following oil spills was to catch and treat oiled birds as soon as possible, before releasing them back into the wild; measures to prevent birds becoming oiled were not part of any oil spill contingency plans (Wolfaardt 2004). However, given the severity of the *Treasure* spill and the potential for unmanageable numbers of penguins to become contaminated, it soon became apparent that additional measures had to be taken to minimise the number of penguins becoming oiled. However, the idea of fencing breeding colonies to prevent un-oiled penguins from entering the sea where they could potentially become contaminated, was implemented at Dyer Island following the sinking of the *Wafra* in 1971 (Morant *et al.* 1981). During the *Treasure* spill it was not possible, due to the large number of penguins involved, to keep the birds fenced in (or in captivity in the

case of birds from Robben Island, (Crawford *et al.* 2000)) until the oil had been cleared (A.J. Williams pers. comm.). Consequently, a decision was taken to evacuate the birds from Dassen and Robben Islands and release them at Cape Recife, which was considered sufficiently distant (c. 800km to the east) to allow enough time for the oil to be cleaned (Crawford *et al.* 2000). Translocation of penguins to prevent them from becoming oiled had been piloted before for Little Penguins *Eudyptula minor*. In 1995, de-oiled and un-oiled Little Penguins were successfully translocated to sites away from the area that was contaminated after the grounding of the *Iron Baron* in northern Tasmania (Hull *et al.* 1998, Goldsworthy *et al.* 2000).

The greater rates of return and restoration shown by evacuated birds relative to de-oiled birds in this study demonstrate the conservation value of evacuating penguins in large oil spill events. Differences in these variables also highlight the negative impact of oil contamination on African Penguins, particularly on their ability to breed.

The evacuated birds, including the two birds from Dassen Island equipped with satellite transmitters (Percy and Pamela), returned rapidly to their colonies, and many resumed breeding soon after their return. The first evacuated birds were recorded back at Dassen Island on 14 July, 11 days after their release from Cape Recife. The last oil was removed from the *Treasure* on 18 July, but the areas around Dassen and Robben Islands were mostly cleared of oil by 14 July (Crawford *et al.* 2000, R.J.M. Crawford, pers. comm.). The choice of Cape Recife was therefore appropriate in this case because it was sufficiently distant to allow enough time for the oil to be cleared before the birds returned, but close enough for most birds to return within two to four weeks, thereby minimising the disruption to breeding and moult activities (see Chapter Three).

The mean mass of 20 evacuees upon their arrival at Dassen Island was above the average mass for the species (Hockey *et al.* 2005). This suggests that the evacuated birds were able to locate and obtain sufficient food during their return to Dassen Island. Further evidence that the evacuated birds returned in good condition is provided by the rapid restoration of some of the evacuees. Twelve birds resumed breeding by 18 July (i.e. within two days of the first birds having been re-sighted on the island), and an additional 29 had been recorded breeding by the end of August 2000. Of the 12 birds recorded breeding by 18 July, eight were recorded incubating eggs, and four were

observed with chicks. It is likely that in at least some of these cases the mate of the evacuated bird had not been evacuated or oiled and had continued incubation and chick-rearing activities alone (Chapter Three), an observation that was also recorded following the *Apollo Sea* spill (Underhill *et al.* 1999), and the Cape Town Harbour spill in 1998 (Whittington 2000).These breeding attempts were not monitored, but the resumption or initiation of breeding by these birds suggests that they were not in poor condition (Darby & Seddon 1990, Chastel *et al.* 1995, Catry *et al.* 1998, Davis & Renner 2003).

The overall proportion of evacuated birds that were recorded breeding during the study period was more than double the proportion of de-oiled birds that were recorded breeding. This difference is likely to result from a number of factors. Firstly, the evacuated birds were, on average, away from the island for a shorter period (two to three weeks) than the birds that were de-oiled (an average of six weeks between being captured oiled and being released after treatment at SANCCOB). Directly or indirectly, this resulted in evacuated birds returning to Dassen Island more rapidly than de-oiled birds. De-oiled birds may, for example, experience a degree of disorientation following their release from the rehabilitation centre, causing them to move short distances away from their breeding colony before returning there (Whittington *et al.* 2005b). One year after the spill 84% of the total number of evacuated birds re-sighted had been observed, compared with 55% of the de-oiled birds. Consequently, the breeding and moult activities of the evacuated birds would have been less disrupted than was the case for de-oiled birds (see also Chapter Three). Secondly, the evacuated birds were un-oiled and so did not suffer any of the potentially harmful biological impacts of oiling (Bourne 1976, Burger 1992, Burger & Fry 1993, Nisbet 1994, Burger 1997, Burger & Gochfeld 2002, Chapter Two). Oil contamination and the de-oiling process following the *Apollo Sea* spill in 1994 resulted in delayed and reduced breeding for some penguins, while others were never recorded breeding again (Chapter Two).

Another factor which may have influenced the difference in the proportions of evacuated and de-oiled birds recorded breeding is the incidence of transients (i.e. non-residents) in the two groups. The evacuated birds were collected from within fenced breeding colonies, whereas almost all of the oiled birds were caught along the coastline. When oiled, African Penguins generally make landfall at the nearest site (Underhill *et al.* 1999),

and so oiled birds collected at Dassen Island (and Robben Island) may have been residents at other locations. That a much lower proportion (1.6%) of the re-sighted Dassen Island evacuees was observed at other colonies than de-oiled birds (28%) suggests the presence of transients within the de-oiled group. However, between July 2000 and March 2005, the proportion of evacuated birds re-sighted each year that were recorded breeding was between 1.5 and 12 times the proportion for de-oiled birds. The difference was greatest in the first two years following the spill, which may be due in part to the effect of transients, but also to the delayed breeding of de-oiled birds. Further evidence for real differences in these proportions was provided by the CMR models, which, after accounting for transients, indicated significant differences in the probability of breeding between evacuated and de-oiled birds. The difference was most marked in the interval 2000-2001, when 44% of the evacuated birds that had returned to Dassen Island were predicted to have bred, compared with 12% of de-oiled birds.

The CMR models also suggested that breeding activities exerted a greater cost to de-oiled birds than evacuated birds. The estimated survival rates for de-oiled and evacuated nonbreeders were similar. However, the de-oiled birds survived less well once they started breeding. As was reported for de-oiled survivors of the *Apollo Spill*, the adverse effects of oil contamination may become more apparent as a result of breeding activities (Chapter Two), especially the energetically demanding requirements of chick-rearing (Ricklefs 1974, 1983). Reproduction has also been shown to impose a greater cost, as measured by changes in body mass after breeding, to de-oiled Little Penguins than to un-oiled birds in the two seasons following the *Iron Baron* spill (Giese *et al.* 2000, Goldsworthy *et al.* 2000). De-oiled African Penguins from the *Treasure* spill also had a higher probability of stopping breeding (i.e. becoming a secondary nonbreeder) than evacuees, which probably also reflects higher reproductive costs brought about by oil contamination. Breeding success of de-oiled *Treasure* birds was not measured in this study. However between 2001 and 2005 at Robben Island, the mean fledging success of de-oiled *Treasure* birds was 18% lower than un-oiled birds (both those with flipper bands and those without), a difference that was prevalent in every year of the study (Barham *et al.* 2007). The reduced fledging success of de-oiled birds relative to un-oiled birds was driven largely by increased mortality during the period of peak energetic demand by medium to large sized downy chicks (Barham *et al.* 2007), providing further evidence that de-oiled birds experienced greater stress during chick rearing than un-oiled birds.

Of the un-oiled penguins evacuated from Robben Island, 40% had been re-sighted by the end of December 2004, approximately four and a half years after the spill (Barham *et al.* 2006). This proportion is substantially less than the proportion (75%) of those evacuated from Dassen Island that had been re-sighted there by March 2005. It is also less than the proportion (67% of those in adult plumage when oiled) of de-oiled birds estimated to have been from Robben Island that were re-sighted there over the same time period (Barham *et al.* 2006). Given the demonstrated impacts of oil contamination on African Penguins, (Barham *et al.* 2007, Chapters Two, Three and Five), it is surprising that, in contrast to the results at Dassen Island, a greater proportion of the de-oiled birds from Robben Island were re-sighted than evacuated birds. The penguins evacuated from Robben Island experienced a substantially higher mortality rate between their capture on the island and their release at Cape Recife than the penguins evacuated from Dassen Island. This was almost certainly due to the different types of vehicles used to transport the birds from the Western Cape to Cape Recife. The Dassen Island birds were transported in open-tiered sheep trucks, whereas the Robben Island birds were placed in closed trucks with less ventilation. Post-mortem examination of the birds that were found dead at Cape Recife revealed that the deaths were probably caused by carbon monoxide poisoning (Crawford *et al.* 2000). Another difference between the birds that were evacuated from Robben and Dassen Islands was the way in which they were held before being transported to Cape Recife. The Dassen Island birds were fenced in at the island, whereas the Robben Island birds were transported off the island and kept in a holding facility on the mainland before being re-packed into penguin boxes and trucked to Cape Recife (Crawford *et al.* 2000). The extra handling of the Robben Island birds and the captive conditions at the holding facility may also have contributed to the higher level of mortality amongst the Robben Island birds at Cape Recife.

Although these factors may help explain why a larger number of Robben Island evacuees than Dassen Island birds died during the road trip to Cape Recife and soon thereafter, it cannot account for the overall difference in the proportions of de-oiled and evacuated birds re-sighted at Robben Island. It also cannot account for the discrepancy between the proportions of evacuated birds re-sighted at the two islands. The fact that 30% of the Robben Island evacuees were observed at Dassen Island, whereas only 1% of the Dassen Island evacuees were observed at Robben Island, suggests that a large

proportion of the un-oiled birds evacuated from Robben Island may have been transient visitors to the island when they were caught. The un-oiled penguins evacuated from Robben Island were caught along the shore (Barham *et al.* 2006), whereas those from Dassen Island were from within the breeding colonies and so are more likely to have been resident breeders, and therefore more likely to have returned rapidly to the colony. The presence of non-resident penguins at Robben Island following the *Treasure* oil spill is highlighted by the fact that the number of penguins removed from the island following the *Treasure* spill exceeded the estimated population of the colony in 2000 by more than 4 000 individuals (Crawford *et al.* 2000). It is noteworthy that, excluding birds that were observed at both islands, the proportion of Robben Island evacuees re-sighted on Dassen Island that were recorded breeding there was similar to the proportion of re-sighted Dassen Island evacuees recorded breeding. If the transient visitors that were collected at Robben Island returned to their resident colony following release, as would be expected, the proportion of released birds re-sighted would be biased low. Including the Robben Island evacuees that were re-sighted at Dassen Island alone (i.e. excluding birds observed at both islands) increases the total proportion of these birds that were re-sighted to 65%, similar to the 69% of de-oiled penguins observed at Robben Island over the same period (Barham *et al.* 2006), but less than the 75% of Dassen Island evacuees that were re-sighted. Because re-sighting effort after the *Treasure* spill was largely limited to Dassen and Robben Islands, it is not possible to determine the degree of movement or return of birds to other colonies. It is also worth noting that the nesting habitats at Dassen and Robben Islands differ, which in turn influences the re-sighting probability of banded individuals at the two colonies. For example, parts of Robben Island are infested with dense stands of *Acacia cyclops* shrubs and trees, under which penguins breed. These birds are generally more difficult to detect than birds nesting in more open colonies, which are more characteristic of Dassen Island. This demonstrates the importance of accounting for recapture probabilities in estimating survival and related parameters (Lebreton *et al.* 1992).

Lightly oiled penguins

The proportion (59%) of lightly-oiled adult penguins (i.e. not de-oiled) that were re-sighted at Dassen Island from 2001 to March 2005 was less than the proportion (75%) of (un-oiled) evacuated birds that were re-sighted during the same period. It was also less than the proportion of de-oiled adult penguins estimated to have been from Robben

Island that were re-sighted there by the end of 2004 (Barham *et al.* 2006). The re-sighting probability of penguins with less than 5% oil contamination was similar to that of un-oiled birds. However all penguins with more than 5% of their bodies covered in oil had significantly lower re-sighting probabilities compared with un-oiled birds.

The overall proportion (23%) of re-sighted lightly-oiled adult penguins that was subsequently recorded breeding at Dassen Island was less than the proportion (30%) of de-oiled penguins recorded breeding during the study period, which in turn was less than half the proportion of evacuated birds that were recorded breeding. The differences were greatest in 2000, when no lightly oiled penguins were recorded breeding, and 2001, when the proportion of re-sighted lightly oiled penguins that were recorded breeding was half that of de-oiled penguins. This difference suggests a longer delay in restoration for lightly-oiled birds, and confirms that even low levels of contamination are harmful to African Penguins. It also highlights the importance of de-oiling all contaminated penguins. In contrast to the re-sighting probabilities, even penguins with less than 5% oil coverage had a significantly lower probability of resuming breeding than un-oiled birds.

It is apparent that the original extent of oiling was an important factor influencing both survival (inferred from the re-sighting probabilities) and restoration success (proportion of re-sighted birds recorded breeding). A larger proportion of penguins with 5% or less of their body covered in oil was re-sighted and recorded breeding than penguins with more extensive oiling. Similarly, the proportion of juvenile penguins re-sighted and recorded breeding was largest for penguins that had 5% or less of their body covered in oil; no juvenile penguins with more than 5% contamination were recorded breeding. The small sample sizes necessitate some caution in interpretation. However, the degree of oiling, and its effect on body mass, was found to be the most important factor determining post-release survival of de-oiled Little Penguins following the *Iron Baron* spill in Tasmania (Goldsworthy *et al.* 2000), and so is likely to be similarly important for oiled African Penguins. In the *Iron Baron* study, the likelihood of post-release survival declined by about 11% per year for every 25% increase in the extent of oiling (Goldsworthy *et al.* 2000). Body mass at capture and the period between capture and de-oiling significantly influence the survival rates of oiled African Penguins through the de-oiling process; birds that are caught at weights less than 2kg have significantly greater mortality rates than those that are heavier than 2kg (Kerley & Erasmus 1987). Interestingly, Parsons &

Underhill (2005) found no correlation between the extent of oiling for African Penguins on admission to SANCCOB in 2001 and 2002 and their probability of surviving the de-oiling process to be released. It is possible that a greater extent of oiling of African Penguins manifests itself in reduced survival and restoration after the birds have been released from SANCCOB. This proposed effect may explain some of the individual variability in survival, restoration and productivity of de-oiled penguins, both within and between spills. For example, those penguins that were never recorded breeding after being de-oiled following the *Apollo Sea* spill (Chapter Two) may have suffered greater levels of contamination than those that were active breeders following the spill. Clearly, this is an area that requires further investigation.

Success of hand-rearing orphaned chicks

Up until March 2005, 20% of the hand-reared chicks that were released with flipper bands had been re-sighted at Dassen Island. This is slightly larger than the proportion (16%) observed at Robben Island until the end of December 2006 (Barham *et al.* submitted). In total 588 individuals (33% of those released) had been re-sighted by the end of December 2006 at the two colonies, 60 (10%) of which were observed at both islands. The total proportion of *Treasure* orphans re-sighted at Robben and Dassen Islands was substantially greater than the proportion (10.8%) of hand-reared chicks that were re-sighted following the *Apollo Sea* spill over a five year period (Whittington & Gildenhuys submitted). In the latter study, the survival rate of hand-reared chicks was similar to that of naturally fledged chicks from Dassen Island (Whittington & Gildenhuys submitted).

That a greater proportion of the chicks released at Robben Island were observed at both Robben and Dassen Islands is of interest. The natal colony of the chicks was not known. All of the chicks that were reared at Monty's rehabilitation centre were released at Dassen Island, and chicks that were raised at SANCCOB and its satellite centres were released at Robben Island. The larger proportion of Robben Island birds re-sighted at both islands suggests that these birds may have experienced a lower mortality rate than those released on Dassen Island. The chicks reared at Monty's (and released on Dassen Island) were routinely released at a heavier mass than even the largest naturally reared chicks (pers. obs). Although the intention of the volunteers at Monty's was to fatten the birds so that they were better equipped to survive once they were released, it

is possible that these birds were "overweight". Juvenile African Penguins are less efficient swimmers than adults (Wilson 1985), and so would be less efficient at evading predators, such as Cape Fur Seals *Arctocephalus pusillus* and sharks (Cooper 1974, Randall *et al.* 1988). Overweight chicks are less agile than those that fledge at an optimum weight, and therefore less likely to escape an attack from a predator.

On the basis of the large degree of mixing of the two groups of hand-reared chicks subsequent to their release, it is clear that chicks do not necessarily recruit to the colony at which they were released. African Penguins are known to be strongly faithful to their natal islands, and generally return there to breed (Randall *et al.* 1987, Whittington *et al.* 2005a). However birds have been reported emigrating as first-time breeders from their natal colony to localities where conditions (generally food availability) are more favourable at the time, and remain faithful to that colony thereafter (Crawford 1998). A recent proposal to bolster extant but declining colonies of African Penguins through introductions to these colonies of chicks reared in captivity (R.J.M. Crawford *in litt.*) requires an understanding of the cues used by penguins to return to their natal island. The results presented here suggest that the release site alone may not be sufficient to determine the locality at which the birds will settle. A greater degree of success may be obtained if chicks were brought to the colonies earlier and kept there for longer before being released. Alternatively, we may have to rely on the penguins themselves to determine the best location at which to breed.

The annual survival rates for hand-reared orphans released at Robben Island but re-sighted at Dassen Island varied during the course of the study (2001–2004). Annual survival was lowest (0.41) for the period 2002–2003, increasing the following year to the highest recorded estimate of 0.79. The estimated survival of *Treasure* hand-reared orphans at Robben Island was just less than 0.50 in 2000 and 2001, and increased to about 0.80 from 2002–2004 (Barham *et al.* submitted). Except for 2002, the survival estimates were similar. The CMR models used to estimate survival in both the Dassen Island and Robben Island analyses did not distinguish between mortality and permanent emigration. It is possible that the lower survival estimate in 2002 for the hand-reared orphans (all of which would have been sub-adults, i.e. not yet of breeding age) re-sighted at Dassen Island, relative to Robben Island, may therefore be due to birds that were first re-sighted at Dassen Island, but subsequently recruited to Robben Island.

Alternatively, the difference in survival estimates may have resulted from different levels of threat (such as predation) faced by the two groups of birds, either at the respective colonies, or in other areas visited by the two groups of birds. Little is known about the movements of sub-adult penguins, and whether there are any differences between birds from Dassen and Robben Islands.

About 9.6% of the hand-reared *Treasure* chicks re-sighted at Dassen Island during the study period were recorded breeding, slightly less than the proportion (c. 15%) that attempted breeding following the *Apollo Sea.* (Whittington & Gildenhuys submitted). In total, 97 (33.8%) of the hand-reared *Treasure* chicks that were re-sighted at Robben Island were recorded breeding by the end of December 2006 (Barham *et al.* submitted). The lower proportion of birds breeding at Dassen Island is likely to be due to the lower re-sighting effort at Dassen Island (relative to Robben Island) from 2003 onwards, when these birds started breeding for the first time. Even though hand-reared chicks survive as well as naturally fledged chicks (Whittington & Gildenhuys submitted) and a reasonable proportion of these birds attempt breeding, and appear to breed as well as other birds (Barham *et al.* submitted), annual survival of first year birds is less than that of adults (Whittington 2002). Furthermore, given the average age of first breeding – 4.6 years at Dassen Island (Whittington *et al.* 2005c) – much fewer hand-reared chicks will recruit into the breeding population than birds already in adult plumage. Thus, when faced with limited resources priority should be given to preventing adults from becoming oiled and de-oiling adult penguins that become contaminated. This will ensure a greater and more rapid rate of restoration, and thereby facilitate the recovery of the population after the spill.

Census results following the *Treasure* spill

Against the background sketched in the Introduction, and the concern about the impact of the *Treasure* oil spill on the breeding population, the results of the 2001 census were surprising. The increase in the number of penguins breeding in 2001 can be attributed to several factors. The combined spawner biomass of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax,* the two most important prey items for African Penguins (Berruti *et al.* 1989, Crawford & Dyer 1995, Crawford *et al.* 2006), in South African waters in 2001 was double any previous estimate obtained by a direct survey (van der Lingen *et al.* 2001, Crawford *et al.* 2006). The abundance of food for penguins in 2001 is

likely to have resulted in a large percentage of birds of breeding age attempting to breed. Indeed, the proportion of re-sighted *Apollo Sea* birds recorded breeding each year between 1994 and 2005, peaked from 2001 to 2003 (Chapter Two). Increased recruitment in the few years before the *Treasure* spill likely also contributed to the growth in penguin numbers. African Penguins recruit to the breeding population at 3–4 years of age, and the four years prior to the 2001 census were markedly better food years than earlier years (Barange *et al.* 1999, van der Lingen *et al.* 2001). The anticipated adverse impact of the *Treasure* spill was therefore fortuitously offset by favourable feeding conditions, which appear to be the result of careful management of the Sardine resource during the two decades prior to the *Treasure* spill (Beckley & van der Lingen 1999), and favourable environmental conditions, which resulted in good year-classes of Anchovy from 2000 to 2003, but especially in 2001 (van der Lingen *et al.* 2001, Crawford *et al.* 2006).

Given the death of about 2 000 adult penguins in the *Treasure* oil spill in 2000 (Crawford *et al.* 2000), and the relatively small proportion of de-oiled birds which attempted breeding in 2001, it is clear that the increased breeding populations observed in 2001 would have been even greater had the oil spill had not occurred. Feeding conditions remained favourable for penguins in the Western Cape up until 2004 (Crawford *et al.* 2006, in prep.). Consequently, numbers of African Penguins breeding in the Western Cape, and especially at Dassen and Robben Islands, continued to increase after 2001, reaching a peak in 2004 (Underhill *et al.* 2006, Chapter Four). It seems that 2002 must have been a particularly good year because it was the period in which the greatest proportion of re-sighted *Apollo Sea* birds (Chapter Two), and all *Treasure* affected birds, were recorded breeding. It was also the year in which the largest breeding success was recorded for African Penguins at Robben Island in a study which spanned the period 2001–2005 (Barham *et al.* 2007).

Subsequently, an eastward shift in the distribution of Sardine (van der Lingen *et al.* 2005, Fairweather *et al.* 2006), and a decline in the biomass of Anchovy (Crawford *et al.* in prep.) has led to a substantially reduced availability of prey for penguins west of Cape Point, and thus a reduction in the breeding population of African Penguins in the Western Cape between 2004 and 2006 of 44.7% (Crawford *et al.* in prep., Chapter Four).

The results reported here highlight the importance of two factors for the future of African Penguins: oiling, and the availability of pelagic fish as a food resource. Better management of the oil pollution problem, and specifically reducing the frequency of oiling incidents and the number of penguins that become oiled, will have a positive effect on the conservation status of African Penguins. However, South Africa is a global oiling hotspot, due mostly to its position on a major international sea route, and so it is reasonable to expect that major oil spills will occur in the future. It is therefore crucial that seabird rescue operations and the de-oiling process continue to be improved, so that the impacts of future spills on the already threatened African Penguin (and other seabirds) can be minimised. Wise management of fish stocks aimed at increasing this resource will have a positive impact on the conservation status of African Penguins. The corollary is that reduced pelagic fish resources, or even a shift in the distribution of prey, may have severe consequences for central-place foragers such as the African Penguin.

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Table 6.1 Numbers of African Penguins transported off Dassen Island during the *Treasure* oil spill, June-July 2000. Oiled birds and orphaned chicks were sent to SANCCOB and satellite rehabilitation centres. Clean adults were evacuated and translocated to Cape Recife.

Date	Oiled adults	Oiled juveniles	Oiled chicks	Clean adults	Orphaned chicks	Mode of transport
25/06/2000	29	15				Boats
26/06/2000	83	29				Boats
27/06/2000	198	103				Boats
28/06/2000	92	51				Boats
29/06/2000	571	59				Boats
30/06/2000	77	26				Boats
01/07/2000	563	211				Boats
02/07/2000				3 580		Boats & Helicopter
03/07/2000				4 735		Helicopter
04/07/2000				4 030	171	Helicopter
05/07/2000	750	152			170	Boats
06/07/2000	212	62			108	Boats
08/07/2000	43	17			108	Boats
10/07/2000	66	29			68	Boats
11/07/2000	39	11	4			Boats
14/07/2000	14	2			82	Boats
17/07/2000	1					Boats
21/07/2000	2	1				Boats
23/07/2000	1					Boats
28/07/2000	3					Boats
TOTALS	2 744	768	4	12 345	707	

Table 6.2 Numbers of lightly oiled African Penguins that were caught, flipper-banded and released at Dassen Island on 8 July 2000. The degree of oiling refers to the extent of the ventral part of the penguin which was oiled. Oil contamination was considered to be "Deep" if it had reached the skin of the bird, and "Superficial" if it had not.

	Adult		Juvenile	
Degree of oiling (%)	Deep	Superficial	Deep	Superficial
<5		79		37
5	1	58	1	25
10	3	34	1	8
15	2	3		2
20		1		
TOTAL	6	175	2	72

Table 6.3 Cumulative numbers of African Penguins re-sighted and recorded breeding at Dassen Island over different time periods following release.

	De-oiled adults			Evacuated adults		
Time elapsed	Number Observed	Number Breeding	*Proportion Breeding (%)	Number Observed	Number Breeding	*Proportion Breeding (%)
Jul 2000 – Aug 2001	1557	247	15.86	644	404	62.73
Jul-2000 - Aug-2002	2248	590	26.25	734	500	68.12
Jul-2000 - Aug-2003	2596	732	28.20	750	518	69.07
Jul-2000 - Aug-2004	2766	832	30.08	763	521	68.28
Jul-2000 - Mar-2005	2818	841	29.84	766	521	68.02

* Cumulative proportion of birds observed at Dassen Island that were recorded breeding there over the different time intervals

Table 6.4 Numbers of adult African Penguins affected by the *Treasure* oil spill observed and recorded breeding at Dassen Island each year, July 2000–March 2005.

	De-oiled birds			Lightly oiled birds			Evacuated birds		
Year	Number observed	Number breeding	Proportion breeding (%)	Number observed	Number breeding	Proportion breeding (%)	Number observed	Number breeding	Proportion breeding (%)
2000[a]	796	30	3.77	52	0	0.00	499	232	46.49
2001	1162	247	21.26	39	4	10.26	518	348	67.18
2002	1145	428	37.38	32	12	37.50	424	298	70.28
2003	636	241	37.89	27	8	29.63	234	149	63.68
2004	486	167	34.36	18	6	33.33	127	65	51.18
2005[b]	94	35	37.23	6	2	33.33	25	15	60.00

a – from July 2000 – December 2000
b – from January 2005 – 16 March 2005

Table 6.5 Numbers of lightly-oiled juvenile African Penguins caught, flipper-banded and released at Dassen Island on 8 July 2000, following the *Treasure* oil spill, which were re-sighted and recorded breeding at Dassen Island between August 2000 and March 2005.

Degree of oiling	$Number banded	Observed		Breeding	
		Number observed	*Proportion observed (%)	Number breeding	#Proportion breeding (%)
<5%	37	19	51	2	10.53
5%	25	14	56	2	14.29
10%	8	3	38	0	0
15%	2	0	0	0	0
TOTAL	72	36	50	4	11.11

* Proportion of banded birds observed during the study period
\# Proportion of the birds observed that were recorded breeding
$ Excludes two juveniles which were "deeply" oiled (see Table 6.2 for further details), because they were not observed after they were banded.

Table 6.6 The number of hand-reared African Penguin chicks that were released from Dassen Island and Robben Island after the *Treasure* oil spill, that were re-sighted and recorded breeding at Dassen Island between 2001 and March 2005.

Release Island	Number released	Number re-sighted	Number breeding
Dassen Island	732	81	8
Robben Island	1 055	280	26
TOTAL	1 787	361	34

Table 6.7 Summary of model selection of multi-state capture-mark-recapture analysis for three groups (g) of African Penguins at Dassen Island, 2000–2004: de-oiled adults, evacuated birds and orphaned chicks (see text for further details). I modelled survival in each breeding state (S_n, S_b, S_s for non-breeder, breeder and secondary nonbreeder, respectively) as well as recapture rates in these states (P_n, P_b, P_s). I also modelled transitions between states (ψ_{nb}, ψ_{bs}, ψ_{sb}, see Figure 2.3). All components were modelled as variable over time (t) or constant (.).The models were assessed using Akaike's Information Criterion (AICc), where a lower value indicates a better model. Δ AICc shows the difference in AICc between the particular model and the best one. The relative performance of each model compared to the other ones in the set is measured by the Akaike weight (*w*). *K* is the number of parameters. The deviance is the difference in –2 log likelihood between the current model and the saturated model, the latter being the model with the number of parameters equal to the sample size.

	Model	AICc	Δ AICc	Akaike Weights (*w*)	*K*	Deviance
1	$\{S_n(g*t\_trans:de\text{-}oiled,orph)S_b(g*t\_orph:const)S_s(g)P_n(.)P_b(.)P_s(t)\psi_{nb}(t*g)\psi_{bs}(g)\psi_{sb}(g)\}$	10525.10	0.00	0.892	52	503.40
2	$\{S_n(g*t\_trans:all)S_b(g*t\_orph:const)S_s(g)P_n(.)P_b(.)P_s(t)\psi_{nb}(t*g)\psi_{bs}(g)\psi_{sb}(g)\}$	10530.18	5.08	0.070	55	502.36
3	$\{S_n(g*t\_trans:all)S_b(g*t\_orph:const)S_s(g)P_n(t)P_b(.)P_s(t)\psi_{nb}(t*g)\psi_{bs}(g)\psi_{sb}(g)\}$	10531.43	6.33	0.038	57	499.53
4	$\{S_n(g*t\_trans:all)S_b(g*t\_orph:const)S_s(g)P_n(t)P_b(.)P_s(t)\psi_{nb}(t*g)\psi_{bs}(.)\psi_{sb}(.)\}$	10545.05	19.95	0.000	55	517.23
5	{breeder-survival:de-oiled=evacuees, otherwise like model 1}	10545.08	19.97	0.000	48	531.51
6	$\{\psi_{nb}$:deoiled=evacuees, otherwise like model 1}	10581.79	56.68	0.000	48	568.22

Table 6.8 Counts of numbers of breeding pairs of African Penguins at South African colonies in 2000 and 2001. Updated from Wolfaardt *et. al.* (2001).

	2000		2001		Percentage Change
WEST COAST					
Lambert's Bay	05 June	11	13 August	15	36.36
Malgas Island	19 April	48	11 June	55	14.58
Marcus Island	22 April	96	21 April	114	18.75
Jutten Island	21 April	898	20 April	1338	49.00
Vondeling Island	19 April	528	18 April	649	22.92
Dassen Island	22-27 April	17042	17-24 April	21409	25.62
Robben Island	17 May- 14 June	5705	16-23 June	6723	17.84
Total		24328		30303	24.56
FALSE BAY-CAPE AGULHAS					
Boulders	12 June	949	21 June	1054	11.06
Seal Island	10 November	52	22 October	56	7.69
Stony Point	12 May	104	20 June	111	6.73
Dyer Island	13 May	2220	19-27 March	2088	-5.95
Geyser Rock		no count		no count	
Total		3325		3309	-0.48
EASTERN CAPE					
Jahleel Island	30 May	538	no count		
Brenton Island	30 May	32	no count		
St Croix Island	30 May	15211	17 May	16950	11.43
Seal Island	31 May	433	30 May	345	-20.32
Stag Island	31 May	24	30 May	24	0.00
Bird Island	31 May	4093	01 May	5376	31.35
Total		19761*		22695	14.85
South African Total		47414		56307	18.76

* excludes counts for Jahleel Island and Brenton Island.

Figure 6.1 Map of Dassen Island, showing the monitoring and management areas (A-I), the location of infrastructure, the position of the interior wall that was used to prevent African Penguins from accessing the coast, and the additional areas that were fenced for the same purpose.

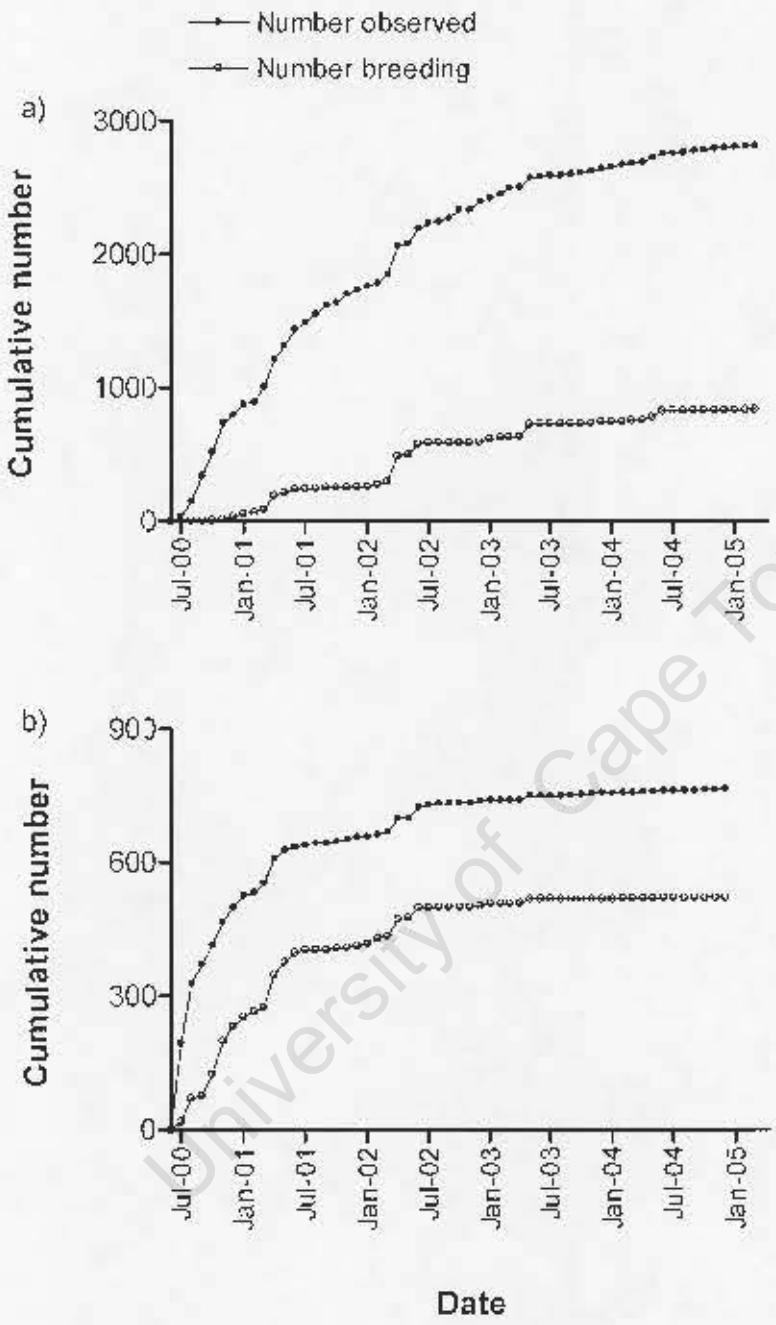


Figure 6.2. Cumulative number of adult a) de-oiled and b) evacuated African Penguins at Dassen Island re-sighted and recorded breeding at Dassen Island for the period July 2000 to March 2005.

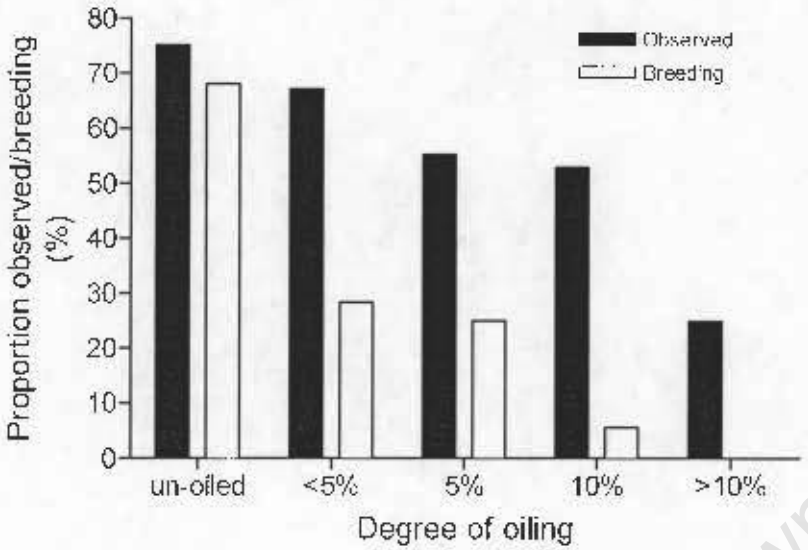


Figure 6.3 Proportion of flipper-banded adult African Penguins from the *Treasure* oil spill with different degrees of oiling that were observed and recorded breeding at Dassen Island between August 2000 and March 2005. These oiled penguins were not sent to SANCCOB, but released at Dassen Island without being de-oiled. The un-oiled group comprises flipper-banded penguins that were evacuated from Dassen Island during the spill, and serves as a control (see text for further details).

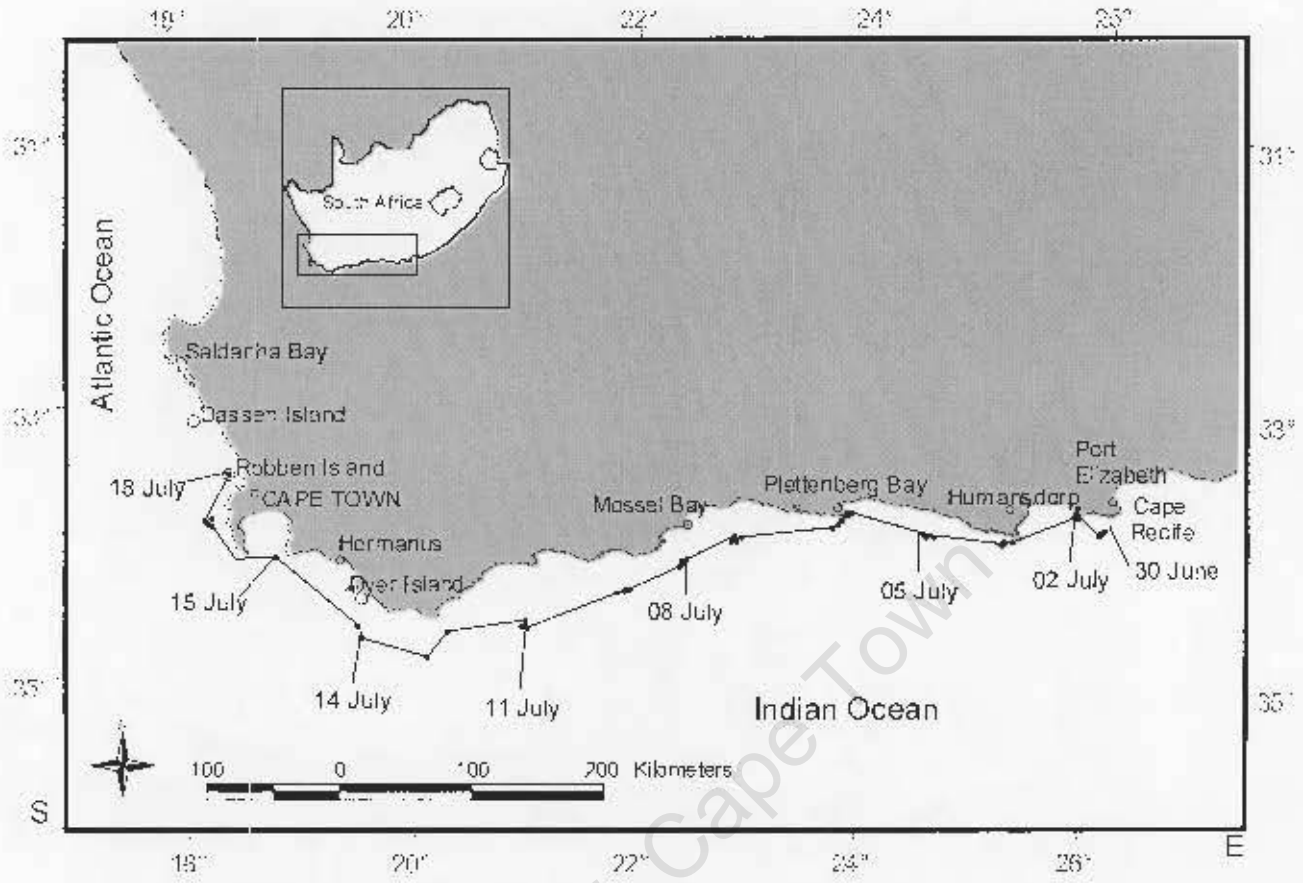


Figure 6.4a Return route of one of the un-oiled African Penguins equipped with a satellite transmitter ("Peter") that was evacuated from Robben Island and translocated to Cape Recife following the *Treasure* oil spill. The bird was released from Cape Recife on 30 June 2000.

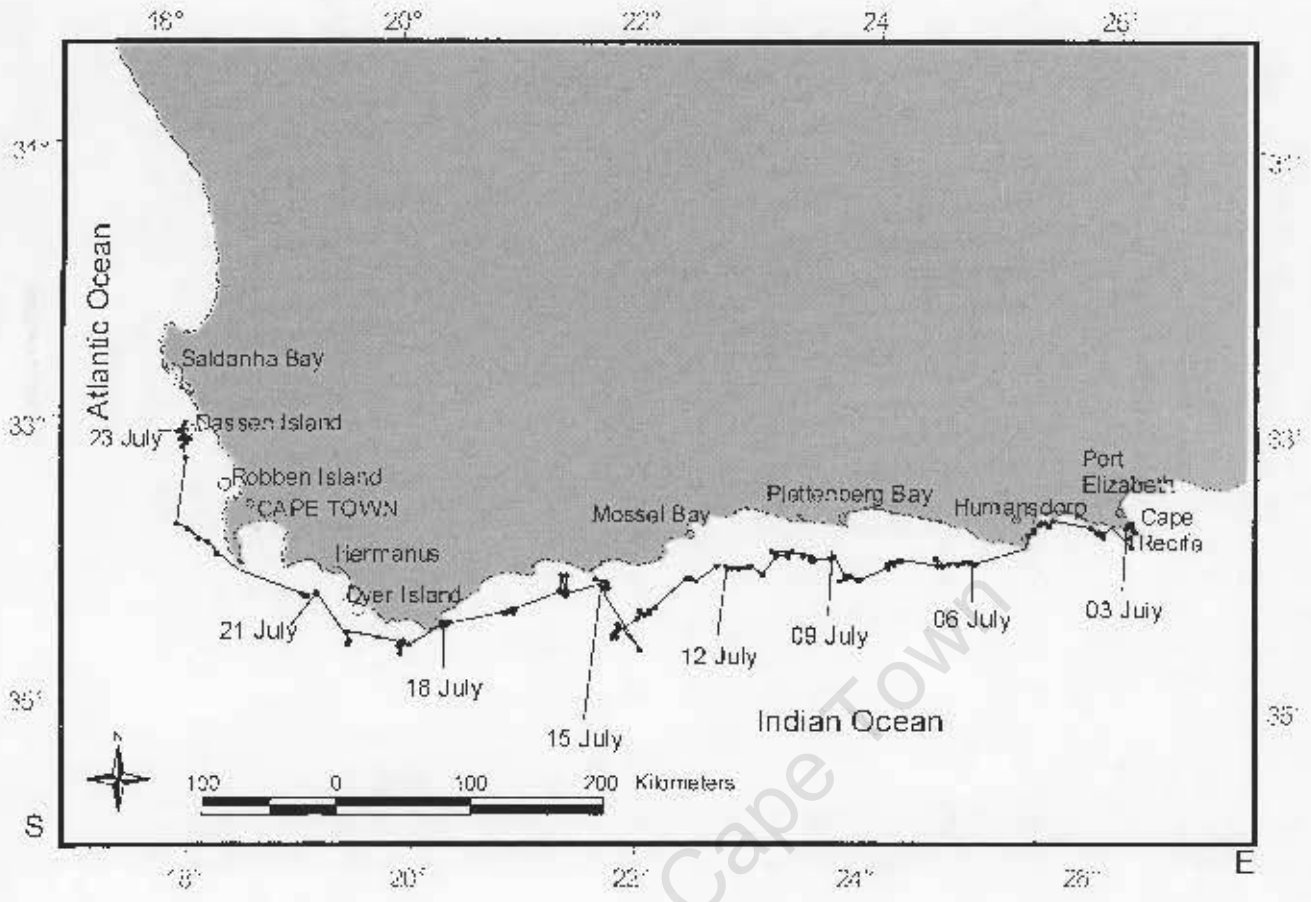


Figure 6.4b Return route of one of the un-oiled African Penguins equipped with a satellite transmitter ("Pamela") that was evacuated from Dassen Island and translocated to Cape Recife following the *Treasure* oil spill. The bird was released from Cape Recife on 3 July 2000.

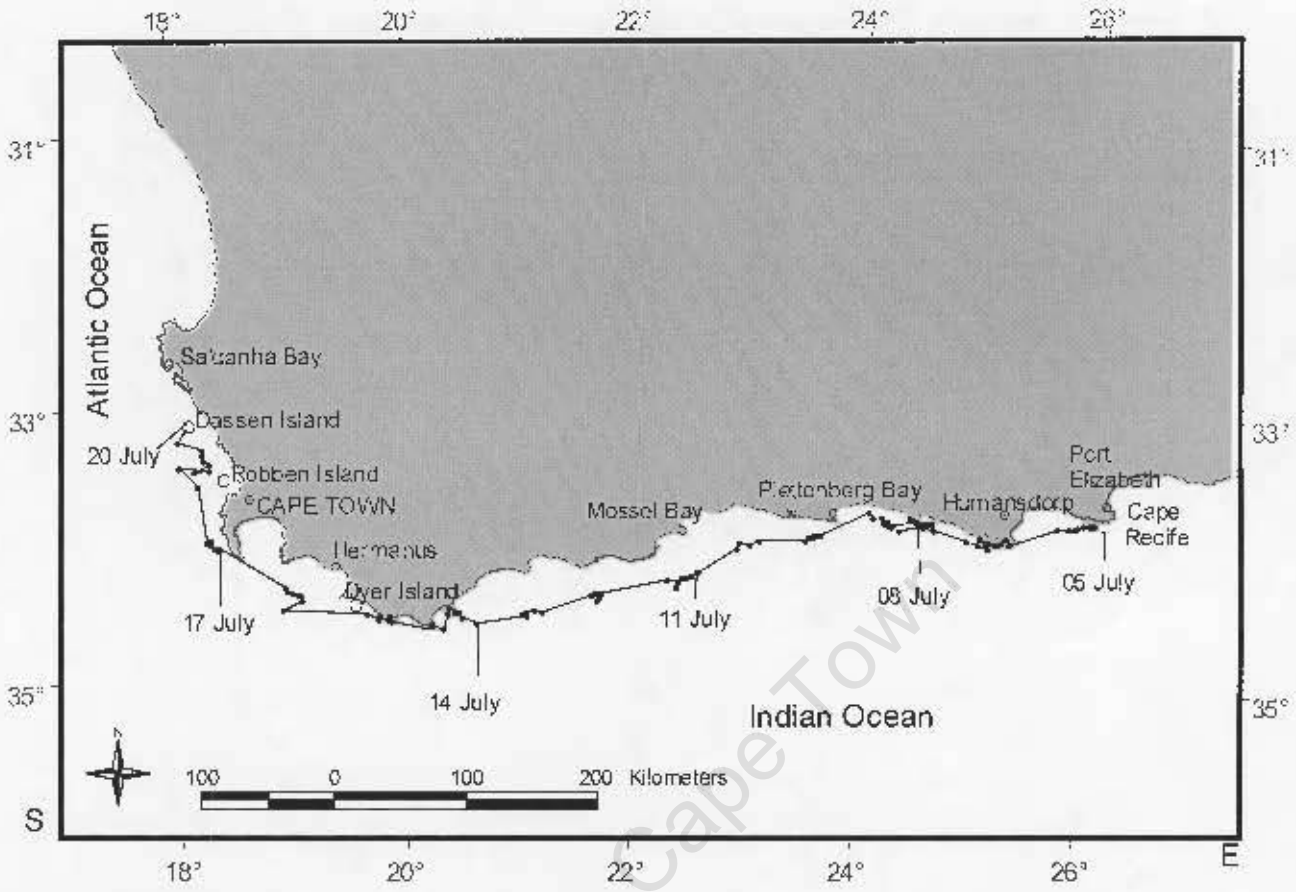


Figure 6.4c Return route of one of the un-oiled African Penguins equipped with a satellite transmitter ("Percy") that was evacuated from Dassen Island and translocated to Cape Recife following the *Treasure* oil spill. The bird was released from Cape Recife on 5 July 2000.

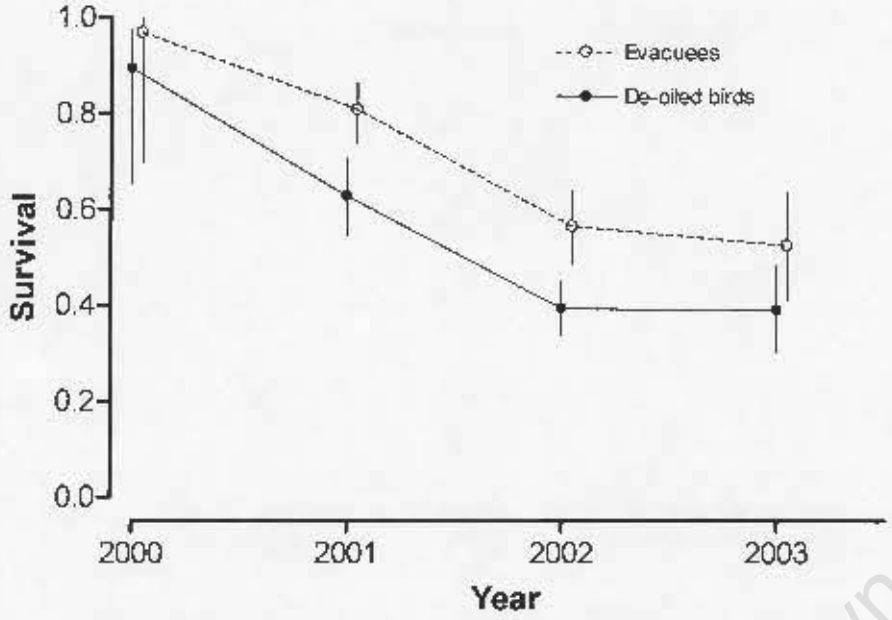


Figure 6.5 Annual survival rates of de-oiled and un-oiled evacuated African Penguin breeders following the *Treasure* oil spill from 2000 to 2004. The year 2000 corresponds to the period July 2000 to February 2001; 2001 comprises the period March 2001 to February 2002, as is the case for 2002 and 2003. The vertical lines show 95% confidence intervals. The estimates are from Model 1, Table 6.7. The symbols are slightly offset to facilitate comparison.

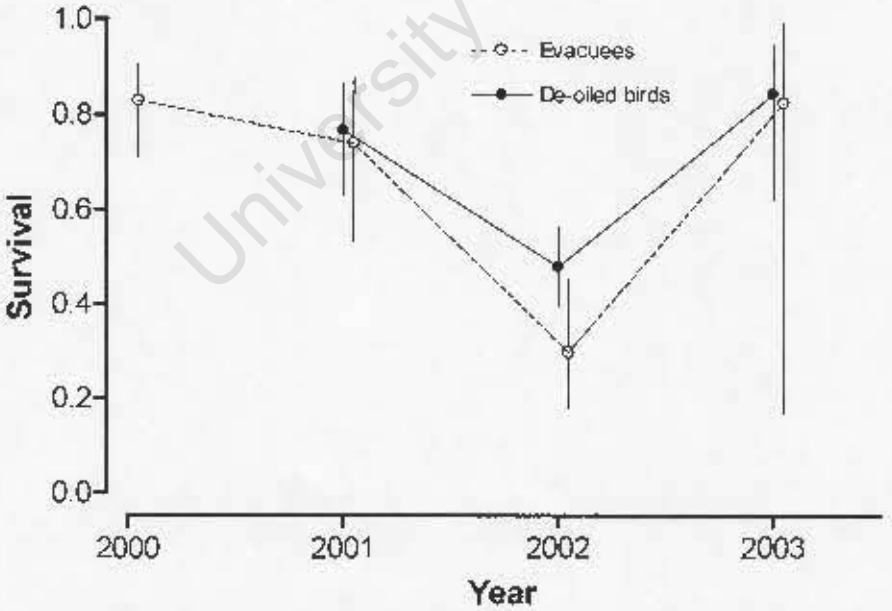


Figure 6.6 Annual survival rates of de-oiled and un-oiled evacuated African Penguin nonbreeders following the *Treasure* oil spill from 2000 to 2004. The intervals for each year are as described in Figure 6.5. Survival could not be estimated for de-oiled nonbreeders in the first year following the spill (2000-01) because of the effect of transients on survival (see text).The vertical lines show 95% confidence intervals. The estimates are from Model 1, Table 6.7. The symbols are slightly offset to facilitate comparison.

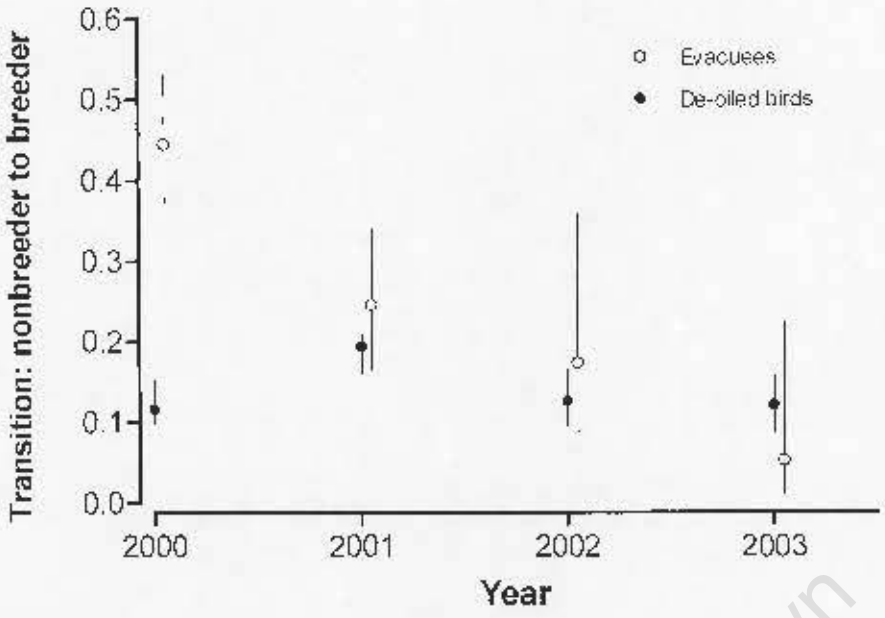


Figure 6.7 Estimates of the probability of transition from nonbreeder to breeder state (ψ_{ns}) for de-oiled and un-oiled evacuated African Penguins following the *Treasure* oil spill from 2000 to 2004. The time periods for each year are as described in Figure 6.5. For each year, the probability of becoming a breeder applies to those birds that have not yet been recorded breeding. The vertical lines show 95% confidence intervals. The estimates are from Model 1, Table 6.7.

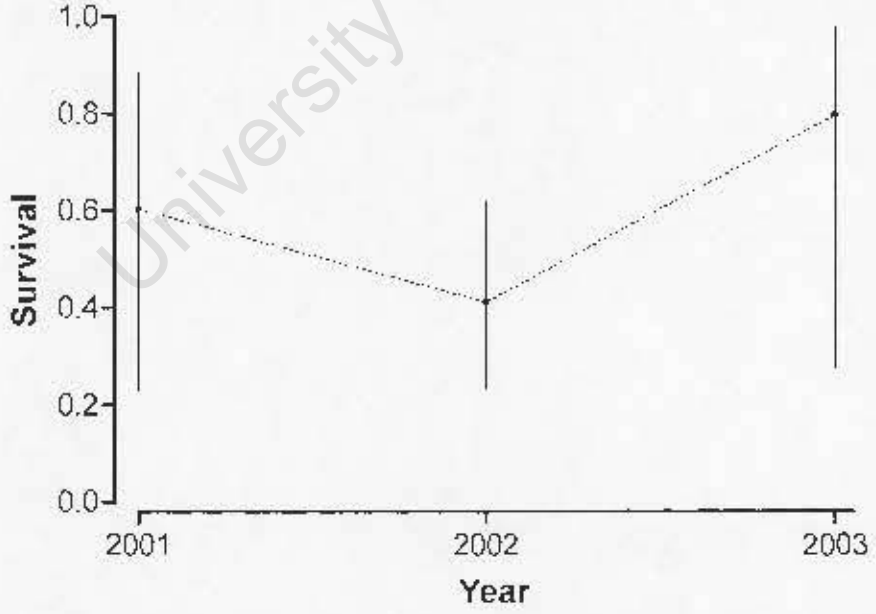


Figure 6.8 Annual survival rates of hand-reared African Penguin chicks at Dassen Island from 2001 to 2003. The analysis is restricted to chicks that were orphaned in the *Treasure* spill, hand-reared at SANCCOB and released at Robben Island. The periods included in each year are provided in Figure 6.5. Survival could not be estimated in the first year following the spill (2000-01) because of the effect of transients on survival (see text). The vertical lines show 95% confidence intervals. The estimates are from Model 1, Table 6.7.

Appendix 6.1 Protocol for the stabilisation of oiled African Penguins at Dassen Island. This is a section of the Seabird Rescue Plan for oiled seabirds at Dassen Island (Wolfaardt *et al.* 1998), and serves to outline the treatment that all oiled penguins which were collected at Dassen Island following the *Treasure* spill received before being transported to SANCCOB.

Introduction

Birds succumb to the effects of contamination in a number of ways:

- Oil on the feathers will impair water repellence, and other insulative properties. Hypothermia sets in as the bird is exposed to external water and air temperatures.
- The penguins will instinctively bathe or preen, and in doing so will ingest oil and toxic pollutants. Poisoning can have both long and/or short-term effects.
- Penguins lose their buoyancy, and can drown if they don't reach dry land.
- Contaminated penguins are unable to hunt for food. No fluids are taken in and dehydration as well as starvation can set in.

By the time penguins are captured, they are dehydrated, exhausted and either extremely hot or cold. The climatic conditions that may exist during a rescue and recovery operation may make it difficult to organize transport from the Island. It may then become necessary to stabilize the birds so as to neutralize the initial affects that the oil may have on them, while they await transport. However, even if transport is immediately available, it is preferable to stabilize birds before they are transported off the island. There is strong evidence showing that birds have a greater chance of surviving the rehabilitation process if they are stabilized before being transported (SANCCOB, unpubl. data). Quite simply, stabilization should be seen as only "First Aid" for the penguins. It does not include washing the birds.

Stabilisation consists of four basic components.

1. **Clearing of the mouth, nostrils and eyes**: Heavily oiled penguins sometimes have debris and oil built up in their mouths and nostrils, which can impair their breathing. Prior to anything else, debris should be removed from these areas using cotton swabs, rags and tweezers. Eyes can be flushed out with clear non-medicated saline solution or water, if nothing else is available.
2. **Temperature Regulation**: Normal bird temperatures range between 37°C and 41°C. Birds with temperatures below 37°C should be considered hypothermic. At night, oiled penguins should ideally be housed indoors. When outside, temporary shade facilities should be provided. Temperature taking is not advised as this may lead to further stress to the bird.
3. **Treatment for Dehydration**: It should always be assumed that oiled birds are dehydrated. Fluids should be tube-fed to birds on a regular schedule beginning shortly after capture. This procedure should only be conducted by trained and experienced personnel on the Island.

Protocols

a) Clean out mouth with **betadine mouthwash**, including area under tongue; syringe in 2-5 ml. of **Amphojel** into mouth being careful not to squirt any liquid into the penguin's trachea (breathing hole).
b) Wash out eyes with **tears eyedrops**, and administer **terramycin** cream in and around eyes – use liberally.

c) Administer 20ml **activated charcoal (PPR)** (once off dose), followed by 60-120ml. diluted **Darrows** solution (50ml Darrows to 1l of water). These fluids are given using a syringe and duodenal tube. If the bird is severely dehydrated (this can be ascertained by grabbing the penguin at the back of the neck – if it feels very "tight", i.e. like there is very little flesh, then the bird is badly dehydrated), inject 50ml **ringers lactate** into each side of the neck (100ml in all), using a 19 guage needle.
d) Inject 0.2ml **iron dextrin** into the breast muscle, using a 23 guage needle (once-off injection).

The above tasks must only be conducted by experienced personnel. Treatment of birds should take place three times a day for relatively strong birds and every three hours for weak birds. Once birds have been rehydrated they can receive fish. Fish should not replace the rehydration treatment, but rather be used together with it (i.e. continue administering **Darrows** until the bird leaves the Island for SANCCOB).

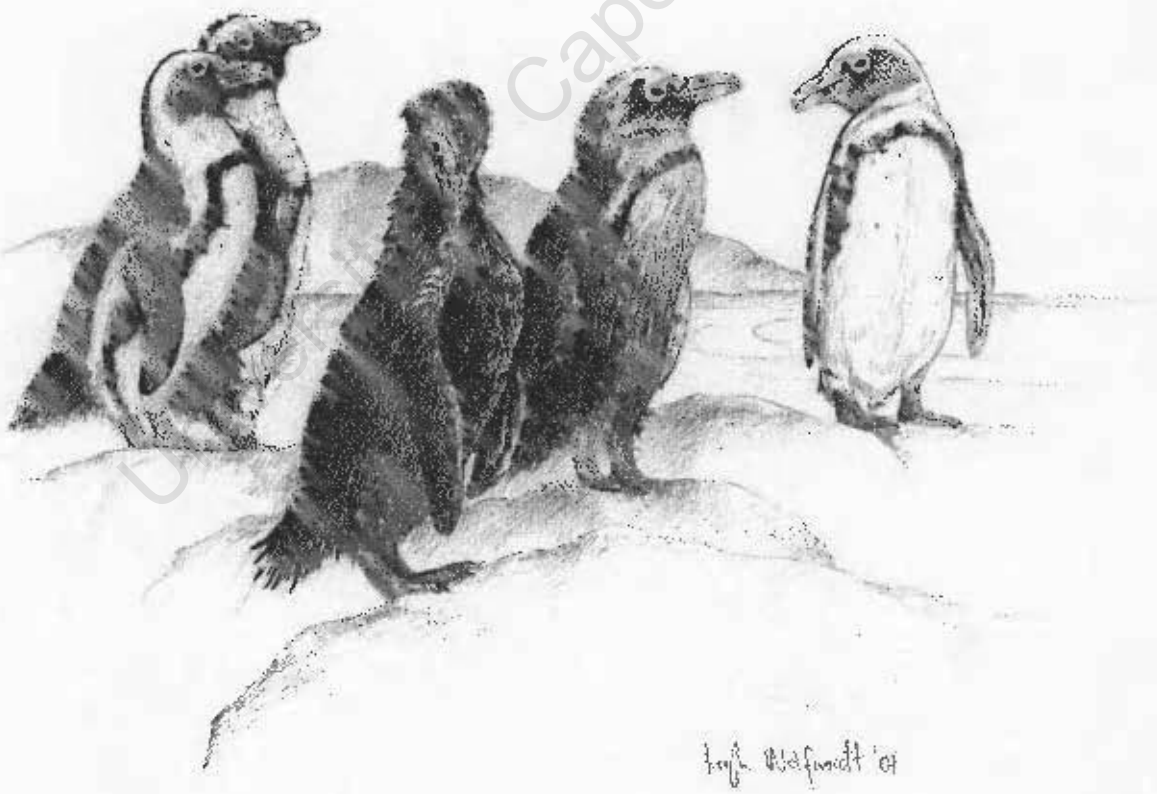
4. **Rest:** By the time oiled penguins are captured they are often in an exhausted state. They will use much of their energy to fight and may look livelier that they actually are. Even so, it is important to assume that oiled birds are suffering from exhaustion. Temperature taking, fluid administration and any other handling should always be done quickly, but carefully, so that the bird can rest. Oiled birds should be kept in the holding pens with good ventilation when not being handled. They should not be disturbed during this time except when being monitored. They need to rest as much as possible.

Stabilisation Facilities

Stabilisation facilities are actually oiled wildlife first aid stations. Their purpose and design is only to provide a place where initial care for oiled birds, immediately following capture and prior to transport, is undertaken. A stabilisation centre has been set up at Dassen Island. This centre should be maintained and kept hygienically clean at all times. During an oil spill event, a Stabilisation Centre Manager will be appointed, who will be responsible for managing activities in the centre and for ensuring that sufficient medical stock is available for the treatment of the oiled birds.

Chapter Seven

The rescue, rehabilitation, and restoration of oiled seabirds in South Africa, especially African Penguins *Spheniscus demersus* and Cape Gannets *Morus capensis*



The rescue, rehabilitation, and restoration of oiled seabirds in South Africa, especially African Penguins *Spheniscus demersus* and Cape Gannets *Morus capensis*

ABSTRACT

South Africa is a global hotspot for oil pollution. The regional oiled seabird cleaning centre (SANCCOB) handled more than 50 000 seabirds between its inception in 1968 and 2005. The majority of seabirds oiled in South Africa were African Penguins *Spheniscus demersus*, followed by Cape Gannets *Morus capensis*, both of which are classified as Vulnerable to extinction. On the basis of the proportion of the total population which had been affected, the African Penguin was considered to have suffered more from oiling than any other seabird species globally. The rehabilitation success (proportion of birds known to have survived for at least one month in the wild) and restoration success (proportion of rehabilitated birds attempting to breed) of de-oiling penguins and gannets were higher than have been reported for any other species. The financial costs of de-oiling African Penguins were substantially lower than the costs of de-oiling seabirds in the northern hemisphere. De-oiling contaminated birds was thus demonstrated to be a valuable conservation intervention for these species, both of which are relatively localised in areas within or close to major shipping routes and ports, where a single spill could threaten a large proportion of the global population. There were, however, long-term effects of oiling on penguins and gannets. De-oiled gannets survived slightly less well than un-oiled birds, but the difference was similar to inter-colony differences in survival. Approximately 27% of rehabilitated African Penguins were unable to breed following their release. In addition, oiling had a long-term negative impact on the breeding productivity and cost of reproduction in de-oiled birds. The primary objective should therefore be to prevent or reduce oil spills in the first place. However, future oil spills are inevitable and the authorities need to ensure that they have plans in place and the required capacity to respond rapidly to spills when they do occur. One of the ways in which to reduce the number of penguins becoming oiled during a spill is to evacuate birds from the affected area. The continued capture and cleaning of penguins and gannets that do become oiled is justified on conservation grounds. Thus, de-oiling should be a twin objective to prevention in South Africa's oil spill management strategy, and every effort should be made to improve further on both of these aspects.

INTRODUCTION

Globally, millions of seabirds have been killed by oil pollution (e.g. Croxall 1975, Bourne 1976, Stowe & Underwood 1984, Piatt & Lensink 1989, Piatt *et al.* 1990, Gandini *et al.* 1994, Underhill *et al.* 1999, Crawford *et al.* 2000b, Goldsworthy *et al.* 2000a, García Borboroglu *et al.* 2006). Oil spill events and the resulting wildlife impacts have increased worldwide during the latter half of the 20th century, coincident with an increase in the international transport of fuel and globalization (Clark 1986). Although oil pollution was recognised as a potential threat to seabirds in the early 20th century, the scientific literature on the subject remained sparse until after World War II (Bourne 1976). The wreck of the *Torrey Canyon* off the coast of England in 1967 stimulated worldwide interest in the subject of oil pollution and especially the potential impacts on marine resources and their conservation (Bourne 1967, 1970a, b). In the *Torrey Canyon* spill some 8 000 oiled birds, mostly Common Murres *Uria aalge* and Razorbills *Alca torda*, were caught; attempts were made to de-oil these birds, but were largely unsuccessful (Clark 1978).

The effects of oil pollution on seabird individuals and populations have been studied extensively and repeatedly reviewed (e.g. Bourne 1968, 1976, Burger & Fry 1993, Nisbet 1994, Burger 1997, Burger & Gochfeld 2002). Not all seabirds are equally vulnerable to oil pollution. Differences in vulnerability between seabirds to oil pollution relate largely to differences in foraging ecology, geographical distribution, breeding phenology, and life-history strategies. Although a wide variety of seabirds may be affected, the greatest impact is on those species which spend a large amount of time in contact with the sea surface, and dive to obtain their prey. In the northern hemisphere, diving birds such as alcids and pelacaniformes are the primary victims of oil spills because they usually occur in large concentrations, spend much of their time in or under the water, and are often concentrated in busy shipping lanes (Vermeer & Vermeer 1975, Stowe & Underwood 1984, Piatt *et al.* 1991, Burger 1992). For similar reasons, penguins and pelecaniformes (primarily gannets) are the most numerous birds affected in the southern hemisphere (Perkins 1983, Berruti 1987, Boersma 1987, Moldan 1989, Gandini *et al.* 1994, Reid 1995, Underhill *et al.* 1999, Crawford *et al.* 2000b, Goldsworthy *et al.* 2000a, Parsons & Underhill 2005, García Borboroglu *et al.* 2006, Altwegg *et al.* submitted). Impacts on seabirds also depend on the nature of the oil spill, which may

differ in the type of oil spilt, and in relation to currents and weather conditions. Consequently, there is little relationship between the volume of oil released and subsequent seabird mortality (Clark 1984, Burger 1993, Whittington 2002).

Although there is general consensus among investigators that large numbers of seabirds are killed as a result of oil spills, there is disagreement, mostly in the northern hemisphere, about the extent to which oil mortality is biologically significant to local, regional and global populations (Bourne 1986, e.g. Piatt & Lensink 1989, Piatt *et al.* 1990, 1991, Parrish & Boersma 1995, Piatt & Anderson 1996, Wiens 1996, Piatt 1997, Piatt & Roseneau 1999). This is partly due to the problems associated with assessing overall mortality attributable to oiling, and then linking these losses to measurable changes in population parameters following spills. Seabird mortality resulting from oil spills is usually estimated from the number of oiled birds found ashore during systematic beached bird surveys, and the proportion estimated to have been lost at sea (e.g. Camphuysen 1998, Camphuysen & Heubeck 2001, Heubeck *et al.* 2003, Roletto *et al.* 2003, Wiese 2003). Uncertainty about the relationship between the number of oiled birds detected onshore and the actual number affected at sea make it difficult to extrapolate reliably from direct counts. Estimates of total mortality resulting from oil spills are thus often imprecise (Piatt *et al.* 1991). Even where total mortality is accurately estimated, it is generally difficult to demonstrate that these losses, and the associated impacts, have contributed towards changes in the population, either because of the lack of reliable pre- and post-spill data, or because of the difficulty in separating oil mortality from other factors, such as environmental variability, natural mortality, recruitment, immigration and emigration, and other sources of anthropogenic mortality (Dunnet 1982, Wiens 1996, Agler *et al.* 1999).

De-oiling contaminated seabirds has generally been viewed as an animal welfare issue, with little conservation value. Proponents of this view argue that de-oiling has little if any impact at the population level due to: 1) the low proportion of oiled birds that are caught alive in a condition that allows them to enter the de-oiling process; 2) limited success of the de-oiling and treatment process resulting in poor release rates from the rehabilitation centre; 3) low survival rates of de-oiled birds after their return to the wild; 4) little evidence of meaningful numbers of de-oiled birds surviving to reproduction; 5) impaired reproductive performance compared with un-oiled birds (for those birds that do breed);

6) demonstrated damage of oil contamination to key organs (Frost *et al.* 1976, Leighton *et al.* 1983, Trivelpiece *et al.* 1984, Fry & Lowenstine 1985, Fry *et al.* 1986, Fry & Addiego 1987, Leighton 1991, Peakall 1992, Boersma 1995, Anderson *et al.* 1996, Sharp 1996, Wernham *et al.* 1997, Newman *et al.* 1999). In addition, the disturbance associated with rescuing oiled seabirds (Boersma 1995, Shannon & Crawford 1999), and the substantial costs associated with de-oiling contaminated wildlife (Estes 1991,1998, Sharp 1996), have led some conservation biologists to suggest that these funds would be better spent on reducing the risks of oil contamination and to bolster populations (and the conservation status) of threatened species, thus minimising their vulnerability to future impacts, including oil spills (Bourne 1970a, Estes 1991, Boersma 1995, Newman 1995).

There are three reasons why southern Africa is of special interest in the study of the effects of oiling upon seabirds. Firstly, the regional oiled seabird cleaning organisation SANCCOB (Southern African Foundation for the Conservation of Coastal Birds) has handled over 50 000 oiled seabirds (SANCCOB unpubl. data), more than any other organization in the world. Secondly, most of the seabirds oiled are endemic African Penguins *Spheniscus demersus* and Cape Gannets *Morus capensis*, and so differ from the seabirds most affected in northern hemisphere spills. And thirdly, southern Africa has the world's most successful record for "rehabilitation" and "restoration" of oiled seabirds (see Chapter One for definitions of these terms).

The focus of this account concerns the population impacts and the rehabilitation and restoration success of penguins and gannets following three major oil spills: the *Castillo de Bellver* spill in 1983, the *Apollo Sea* spill in 1994, and the *Treasure* spill in 2000. Smaller spills that occurred in the interval between the *Apollo Sea* and *Treasure* spills are also considered. These case studies are put into regional perspective through three brief, prefatory reviews. These reviews consider the size and conservation status of the seabird avifauna at risk; the history of oiling in South Africa; and previous work on de-oiling, rehabilitation and restoration of South African seabirds.

REVIEW OF SEABIRDS AT RISK

Southern Africa supports a distinctive seabird avifauna comprising 15 breeding species with a current estimated total population of approximately 385 000 breeding pairs (Table 7.1). This comprises some 60% of the breeding seabirds of sub-Saharan Africa (Cooper *et al.* 1984). In addition more than two million birds of 36 seabird species are annual non-breeding visitors to southern African waters (Berruti *et al.* 1989, Crawford *et al.* 1991).

The vast majority of oiled seabirds treated in South Africa have been African Penguins, which represent more than 90% of the oiled seabirds admitted to SANCCOB between 1968–2005, followed by Cape Gannets, representing just less than 5% of the total (Morant *et al.* 1981, Adams 1994, Underhill *et al.* 1999, Crawford *et al.* 2000b, Whittington 2002, Nel *et al.* 2003, Parsons & Underhill 2005, SANCCOB unpubl. data, Table 7.2). Both these species are of special conservation concern and this section focuses on these two species.

The Cape Gannet has a global population of c. 156 000 pairs but breeds at only six islands, three in Namibia and three in South Africa (Crawford *et al.* 1983, 2007, Crawford 1999). This species is listed as "Vulnerable" in the latest Red Data Book of Birds of South Africa, Lesotho and Swaziland (Barnes 2000) and in the World Conservation Union (IUCN) Red Data list of threatened species (BirdLife International 2004, IUCN 2006), primarily because of a greater than 20% decline in the breeding population during the last 40 years (Crawford 1991, 1999, Barnes 2000). From 1978/79 to 2005/06 the three Namibian colonies declined by 85–98% (Crawford *et al.* 2007). The numbers of gannets at South African colonies remained relatively stable from 1990 to 2000, in contrast to the 78% reduction in numbers at the Namibian colonies during the same period (Crawford *et al.* 2007). However, after 2000 the numbers of gannets breeding at Malgas Island and Bird Island decreased, owing to a reduced availability of prey, especially Sardine *Sardinops sagax*, to birds at these two colonies (van der Lingen *et al.* 2005, Crawford *et al.* 2007).

In addition to food shortages, Cape Gannets have been subject to a number of other threats during the period 2000–2005. These include mortality resulting from

entanglement in fishing gear or as incidental catch on longlines (Cooper & Ryan 2003, Cooper 2006), and increased predation of gannets at breeding colonies, primarily by Cape Fur Seals *Arctocephalus pusillus* (Crawford *et al.* 2001, David *et al.* 2003, Wolfaardt & Williams 2006). The seals have presumably also been affected by the reduced availability of Sardine on the west coast, which may explain why increasing numbers of animals have resorted to preying on seabirds. Other predators of gannets at breeding colonies include Kelp Gulls *Larus dominicanus*, and more recently Great White Pelicans *Pelecanus onocrotalus* (Ryan 2007). Although the number of oiled gannets admitted to SANCCOB during this period was relatively low (223 birds, Table 7.2), the risk of oil pollution incidents in the Western Cape remains a concern (Dernier 1995). Moreover, any mortality and disturbance associated with oil spills would be additive to the factors identified above.

The African Penguin has experienced a substantial decrease in numbers through the 20th century. The estimated population size at Dassen Island (33°25'S, 18°05'E) alone is estimated to have been in excess of 1.45 million birds in the early 1900s alone (Westphal & Rowan 1971, Shannon & Crawford 1999). In the early 2000s, the global population was estimated to be c. 200 000 birds (Crawford *et al.* 1990, 1995b, Hockey *et al.* 2005), a reduction during a century of more than 85%. As a result of its severe and ongoing decline, the African Penguin is currently listed regionally and globally as "Vulnerable" (to extinction) (Crawford 2000a, BirdLife International 2004, IUCN 2006). The species is also listed in Appendix II of both the Convention on Trade in Endangered Species (CITES) and the Bonn Convention for the conservation of migratory species (Underhill 1996). If the rate of decline observed between the 1970s and the 1990s continues, the species is likely to become extinct in the wild during the 21st century (Ellis *et al.* 1998, Whittington *et al.* 2000b). Although numbers of penguins at some breeding colonies increased from the mid 1990s until 2004 (see for e.g. Crawford *et al.* 1999b, Wolfaardt *et al.* 2001, Underhill *et al.* 2006), and three new colonies were established in the 1980s (Crawford *et al.* 1995c, Whittington *et al.* 1996, Crawford *et al.* 2000a) and another in 2003 (Underhill *et al.* 2006), these increases were insufficient to offset the overall downward trend, especially prevalent in Namibia (Crawford *et al.* 2001, Kemper *et al.* 2001). Moreover, the increases in the breeding populations at Western Cape colonies from the mid-1990s, have subsequently been reversed through substantial (>

50%) and rapid decreases in 2005 and 2006 (Chapter Four, Marine & Coastal Management unpubl. data).

A number of factors have contributed to this long-term decline in the numbers of African Penguins. In pristine conditions, penguins dug breeding burrows into prehistoric accumulations of seabird guano. Human excavation of guano for fertilizer forced most penguins to breed on the surface where they are exposed to predators and variable weather conditions (Frost *et al.* 1976, Shelton *et al.* 1984, Kemper 2006). Sustained commercial exploitation of eggs, which, between 1900 and 1930 exceeded 450 000 eggs per year on Dassen Island alone (Frost *et al.* 1976, Siegfried & Crawford 1978), and in 1919 amounted to approximately 600 000 eggs (Wolfaardt 2000, Marine & Coastal Management unpubl. data) substantially reduced recruitment (Frost *et al.* 1976). In the first half of the 20th century African Penguin eggs were harvested at an estimated rate of 48% of total eggs produced (Shannon & Crawford 1999).

The resurgent regional Cape Fur Seal population, which increased from less than 50 000 animals at the end of the 19th century (Butterworth *et al.* 1988) to a level of 1.5–2 million animals at the end of the 20th (Butterworth *et al.* 1995, Best *et al.* 1997), poses considerable threats to African Penguins and Cape Gannets (David *et al.* 2003). Seals out-compete these birds for restricted island breeding space (Shaughnessy 1980, 1984, Crawford *et al.* 1989, 1994) and are significant local predators of the birds themselves (Marks *et al.* 1997, Crawford *et al.* 2001, Wolfaardt & Williams 2006, Ryan 2007). They also compete for shoaling epipelagic fish (Whittington *et al.* 2000b) that are the prime food of the birds (Hockey *et al.* 2005).

Human fisheries, established in the 1950s, also compete for these same fish stocks. Regional trends in the abundance of penguins, as well as breeding success and recruitment, are associated with trends in the abundance and distribution of pelagic fish (Crawford 1998, Crawford *et al.* 1999b, 2001, 2006, Chapter Five). Consequently, large decreases in the sizes of penguin populations have been attributed to scarcity of food (Crawford & Shelton 1981, Crawford 1998). Similarly, the large decreases of gannet populations have been attributed to insufficient food, especially at the Namibian colonies (Crawford *et al.* 1985, 1989, 2007, Crawford 1999).

Lastly, oiling has had a major impact on African Penguins, through direct mortality of adults, juveniles and chicks, reduced breeding productivity of de-oiled birds, and through disturbance associated with rescuing oiled birds (Morant *et al.* 1981, Adams 1994, Shannon & Crawford 1999, Underhill *et al.* 1999, Crawford *et al.* 2000b, Chapters Two, Five and Six). Although the numbers affected are much less than for penguins, oil pollution is also considered to be a major threat to Cape Gannets (Berruti 1987, Crawford 2000b). The potential threat of oiling to these two species must be considered in light of their already reduced population sizes (and ongoing declines), which increase their vulnerability to stochastic events such as oiling. For African Penguins, stochastic models suggest that colonies with fewer than 10 000 breeding pairs have a 9% probability of becoming extinct over 100 years; colonies with less than 100 pairs had a similar probability of extinction over 50 years (Crawford *et al.* 2001). Currently, there are only two African Penguin colonies with breeding populations in excess of 10 000 breeding pairs, both located within busy shipping routes. Almost half of the extant breeding colonies number less than 100 pairs (Crawford *et al.* 2001).

The demographic traits of seabirds such as the African Penguin and Cape Gannet further increase their vulnerability to oil pollution and other threats. Both species are long-lived, exhibit delayed sexual maturity, and low fecundity (Hockey *et al.* 2005), characteristics which generally buffer populations from short-term environmental variability such as fluctuations in food supply (Hamer *et al.* 2002). Theoretically, delayed breeding and great longevity in such seabirds reduces their susceptibility to unfavourable environmental conditions relative to shorter-lived species (Weimerskirch 2002). Fecundity is the main trait of these species affected by variations in environmental conditions (Crawford *et al.* 2006). Delayed breeding and abstinence from breeding during periods of poor resource availability, both features of African Penguins and Cape Gannets (Hockey *et al.* 2005), are generally assumed to form part of a strategy to preserve the potentially long life span of individuals (i.e. maximising long-term survival), thereby optimising lifetime reproductive output (Ricklefs 2000, Hamer *et al.* 2002). These life history traits are adaptive in the context of short-term environmental variability, but make it difficult for populations to recover quickly from losses, especially those that involve indiscriminate and large scale adult mortality, such as in oil spills. However, African Penguins, and Spenisciformes generally, are closer to the "fast turnover" (early age at first reproduction, high fecundity, and lower adult survival and life-

expectancy) side of the life history gradient relative to other seabirds of a similar size or body mass (Hamer *et al.* 2002, Weimerskirch 2002, Chapter Five).

BRIEF HISTORY OF OILING IN SOUTHERN AFRICA

The first evidence of seabird oiling in southern Africa is a photograph of an oiled African Penguin at Dassen Island taken in the 1920s (Kearton 1930). The first major seabird oiling events in southern Africa were in November 1948 and August 1952 and, like most subsequent oiling, involved mainly African Penguins (Green 1950, Rand 1952, 1970). Oiling of seabirds was infrequent in southern Africa until the close of the Suez Canal in 1967. This resulted from a dramatic increase in oil transport around the Cape of Good Hope. Traffic peaked at about 10 000 tanker passages a year (Moldan 1989). Initially most tankers were small, designed to pass through the Suez Canal. Subsequent use of super-tankers reduced the number of tanker passages but increased the potential size of a spill. The increased passage of tankers led to a marked increase in the number of major oil spills along the South African coast (Table 7.3), which has experienced five of the world's top 50 largest oil spills (Daidola 1995). In 1968 alone, there were 11 tanker casualties in South African waters (Moldan & Westphal 1994). Subsequent re-opening of the Suez Canal in 1975, and reduction in global use of oil, have reduced the quantities of oil rounding the Cape of Good Hope to pre-1968 levels (Moldan & Dehrmann 1989).

Tankers have not been the only cause of oil pollution. Break-up of cargo vessels and release of their fuel oil has been a major cause of seabird oiling in southern Africa. Recent examples include the bulk ore-carrier *Apollo Sea*, which released 2 400 tonnes of bunker fuel in 1994 and oiled nearly 10 000 penguins (Underhill *et al.* 1999), the 1996 break-up of the cargo vessel *Cordigliera,* which polluted 1 300 penguins (Table 7.3) and the *Treasure*, another bulk ore carrier, which released approximately 1 400 tonnes of fuel oil, resulting in the contamination of more than 19 000 penguins (Crawford *et al.* 2000b). Although these large oil spill events (in terms of numbers of seabirds affected rather than the amount of oil spilt) present a more critical immediate threat to seabird populations in southern Africa, low-level chronic oiling, resulting from small spills, often of unknown origin (presumed to be due to accidental spillages and the illegal washing of bilges and tanks at sea), also poses a major threat to seabird populations, especially in

the long-term (Shannon & Crawford 1999, Ryan 2003, Parsons & Underhill 2005, see also Table 7.3).

Southern Africa has also experienced seabird oiling from non-petroleum based products. In the 1970s fish-oil spilt during wet-off-loading of catches killed 4 500 Cape Cormorants *Phalacrocorax capensis* at Walvis Bay (22°59'S, 14°31'E), Namibia (Berry 1976). At Lamberts Bay (32°05'S, 18°17'E), South Africa, a similar incident affected 7 000 Cape Cormorants, 700 Cape Gannets and 100 African Penguins (Anon 1974). As a result of these incidents new systems of transferring catches from ship to shore were introduced and no further incidents of large-scale fish-oil pollution of seabirds have been recorded (Cooper *et al.* 1982).

There are two potential additional sources of oil spillage in southern African waters. Local offshore petroleum extraction commenced off Mossel Bay, South Africa, in 1997 (Attwood *et al.* 2000) and may develop off Namibia and elsewhere off South Africa if current or proposed exploration is successful. Also in South Africa, under current negotiation is the increase in tanker and bulk ore-carrier traffic to the port of Saldanha Bay (SRK Consulting 2007) and the development of an oil refinery at the new industrial port of Coega, near Port Elizabeth (van Niekerk 2007). To reach either Saldanha Bay or Port Elizabeth vessels must travel close to important penguin and gannet breeding localities. Over 80% of the African Penguin population breed in colonies that are within 100km of major shipping harbours (Nel *et al.* 2003). Similarly, the three South African gannet colonies are all in close proximity to fishing or commercial ports.

REVIEW OF SEABIRD RESCUE

SANCCOB was founded in November 1968 as a result of the oiling of penguins by tanker spills immediately following closure of the Suez Canal (Westphal & Rowan 1971, Morant *et al.* 1981, Moldan & Westphal 1989, Moldan & Westphal 1994). This volunteer, non-governmental organization, now a Section 21 Company, handled between 200 and 2 000 birds a year during the period 1969 to 1993 (Morant *et al.* 1981, Adams 1994). Almost all oiled birds were African Penguins, except in the 1983 spillage from the *Castillo de Bellver* in which most birds affected were Cape Gannets (Table 7.3).

Subsequent to 1983, SANCCOB has handled more than 35 000 oiled penguins, 78% of which were oiled in the *Apollo Sea* (1994) and *Treasure* (2000) spills (Figure 7.1), and more than 1 200 other oiled seabirds (Tables 7.2 & 7.3; SANCCOB unpubl. data).

Even excluding the large numbers of penguins oiled in the *Apollo Sea* and *Treasure* spills, the incidence of oil contamination of African Penguins has increased during the last 15 years. From 1990 to 2005 an average of 750 oiled penguins were admitted annually to SANCCOB from oiling incidents other than the *Apollo Sea* and *Treasure* spills, equivalent to c. 0.5% of the global population annually. This compares with an annual average of 547 birds between 1970 and 1979, and 343 birds for the period 1980–1989 (Nel *et al.* 2003). The proportion of the global population oiled each year in the 1990s and early part of the 21st century increases to 2% when the birds from the *Apollo Sea* and *Treasure* spills are included (Ryan 2003). The *Treasure* spill alone resulted in the contamination of approximately 12% of the global population of African Penguins (Crawford *et al.* 2000b). An additional 19 500 un-oiled penguins were evacuated from Robben (33°48'S, 18°23'E) and Dassen Islands (Chapter Six); together with the contaminated birds, almost 25% of the total species population at the time were handled during the rescue and rehabilitation operation (Crawford *et al.* 2000b, Nel *et al.* 2003).

In all, over the 35 years from 1970–2005, SANCCOB treated more than 45 000 oiled African Penguins, excluding birds that died within 24 hours after arrival at the rescue station. The African Penguin can, based on the proportion of the entire population that has been affected, be considered to have suffered more from oiling than any other bird species.

The percentage of oiled penguins admitted to SANCCOB that were successfully released after de-oiling varied from 45% to 65% per year between 1970 and 1979 (Morant *et al.* 1981). The annual average release rate increased to 68% in the 1980s, 70% in the 1990s and 85% for the period 2000–2005, which included the *Treasure* oil spill (Figure 7.2). Of the oiled gannets admitted to SANCCOB in 2001 and 2002, 87% were successfully released following de-oiling, compared with 50% of Cape Cormorants admitted (Parsons & Underhill 2005). For African Penguins, Cape Gannets, and other seabirds admitted to SANCCOB, the release rates of contaminated birds following de-oiling tend to be greater than for birds that are admitted for other reasons, normally due

to injury or as a result of being found in a weak condition (Parsons & Underhill 2005). Although the trend of improved release rates for penguins and other seabirds is encouraging, from a conservation perspective, one cannot equate release with success. The conservation success of de-oiling seabirds should be measured by the long-term post-release survival and reproduction of de-oiled birds.

The conservation, but not the humanitarian, value of SANCCOB's efforts in rescuing oiled seabirds was questioned by Frost *et al.* (1976). This led to the production of an appropriately shaped metal flipper band for African Penguins (Jarvis 1970, Cooper & Morant 1981) and attempts to evaluate post-release survival of de-oiled birds. These efforts, which spanned the period 1970–1979 and involved penguins from seven different oiling incidents, resulted in 788 of the 2 656 de-oiled penguins being re-sighted, a rehabilitation rate of 30% (Morant *et al.* 1981). The finding of 158 of the rehabilitated/re-sighted birds on eggs or with young indicated a restoration to breeding of at least 6% of the birds de-oiled and released (Morant *et al.* 1981). Unfortunately Morant *et al.* (1981) did not indicate the degree of search effort involved in their study, and especially the intensity of searches for breeding birds. The data have been considered evidence of full restoration into the breeding population (Morant *et al.* 1981), but have also been interpreted negatively as indicating poor long-term performance of de-oiled birds (Fry & Lowenstine 1985, Fry *et al.* 1986, Nisbet 1994, Boersma 1995).

RESTORATION OF CAPE GANNETS OILED IN THE *CASTILLO DE BELLVER* SPILL AND THE SIGNIFICANCE OF OIL EFFECTS ON POPULATION DYNAMICS

The tanker *Castillo de Bellver* caught fire and broke apart about 24km west of Saldanha Bay, South Africa in August 1983. Of the approximately 252 000 tonnes of crude oil on board, an estimated 160 000–190 000 tonnes spilt into the surrounding water (Schumann 1984, Moldan *et al.* 1985). This volume of oil spilt was five times larger than the next largest oil spill in southern African waters (resulting from the collision of the tankers *Venpet* and *Venoil*, near Cape St. Francis in 1977 (Moldan *et al.* 1979)) and was over 100 times the volume of oil spilt following the sinking of the *Treasure* (Table 7.3). The prevailing winds were southerly to south-easterly, which moved the oil away from the coast (and important seabird breeding colonies) northwards into feeding areas of

Cape Gannets off Cape Columbine (Moldan *et al.* 1985). In the context of southern African oil spills, the *Castillo de Bellver* was unique in that the greatest proportion of seabirds affected comprised Cape Gannets, rather than African Penguins. At Bird Island, Lamberts Bay 194 oiled gannets were captured and at Malgas Island (33°03'S, 17°55'E) 1 297 of the estimated 5 000 oiled birds were caught (Berruti 1987). In total, 65% of the oiled birds that were collected were successfully de-oiled and released; all de-oiled birds were released at Marcus Island (33°02'S, 17°58'E), in Saldanha Bay, between 22 August and 23 November 1983 (Moldan 1989), 854 of which were banded (South African Bird Ringing Unit, SAFRING, unpubl. data). There are two sources of information on the subsequent fate of these birds: recovery of dead banded birds and control or re-sighting of live banded birds.

Most (>80%) Cape Gannets attain full adult plumage by three years of age (Jarvis 1972). Average longevity of breeding adults has been estimated as 13–14 years (Crawford 1999), with a maximum recorded longevity of 30.5 years (SAFRING, unpubl. data). The initial sample of gannets was of unknown age, but all were of adult plumage and so at least three years old. On the basis of the above estimation of longevity, the contaminated birds may have ranged in age from three to 25 years. The overall recovery rate for banded Cape Gannets (the percentage of bands ultimately reported to SAFRING), for which there are more than 1000 band recoveries, is 1.3% (SAFRING unpubl. data). Most recoveries are of birds in their first year (Klages 1994, SAFRING, unpubl. data). Between 1983 and 1996, 16 of the banded de-oiled gannets were found dead (SAFRING unpubl. data), a recovery rate of 1.87%, which is slightly higher than the normal mortality rate for un-oiled birds. Four birds died within one month of having been released; the remainder of the recoveries occurred between 15 and 147 months after release (SAFRING unpubl. data). The causes of death of de-oiled birds after release are not well understood (Anderson *et al.* 1999, Newman *et al.* 1999), but it seems likely that the early recoveries were due to the effects of contamination, perhaps acting in concert with potential impacts of handling while in captivity (Newman *et al.* 2004). Birds that were recovered after 15 months (75% of those recovered) can be considered to have been successfully rehabilitated. That only four birds were recovered dead within a month of their release suggests that mortality of de-oiled gannets in the period immediately following release was minimal.

Re-sighting of banded birds provides a more substantial body of information. In 1989, the then Sea Fisheries Research Institute (S.F.R.I.) of South Africa (now Marine & Coastal Management, or M.C.M.), which had banded gannets over several years at Bird Island, Lamberts Bay and at Malgas Island, began a re-sighting program which continued through 2005.

Between 1989 and 2005 a total of 19 516 gannet re-sightings were recorded, comprising 5 726 individuals at Malgas Island, and 4 832 at Bird Island (Altwegg *et al.* submitted). In total, 162 de-oiled gannets from the *Castillo de Bellver* spill were observed during this period, 138 at Malgas Island and 24 at Bird Island. Capture-mark-recapture models show that at both islands, the de-oiled birds that returned to their colonies had slightly lower survival rates than un-oiled birds at the respective colonies (Altwegg *et al.* submitted), consistent with the recovery results. Mean annual survival of de-oiled gannets at Malgas Island and Bird Island was 0.855 and 0.880, respectively; the comparative survival rates for all un-oiled banded birds at these respective colonies was 0.878 and 0.896 (Altwegg *et al.* submitted). At both islands, the slightly lower survival rates of de-oiled gannets was prevalent in each year of the study (Altwegg *et al.* submitted). The difference in survival between de-oiled and un-oiled birds was similar to the difference between the two colonies. There was no evidence that de-oiled birds had a lower probability of breeding than un-oiled birds. However, for all gannets (de-oiled and un-oiled), there was an overall negative trend in the breeding probability during the course of the study, especially at Bird Island (Altwegg *et al.* submitted). Although this downward trend in breeding probability is unlikely to have resulted from the *Castillo de Bellver* spill and other oil pollution incidents alone, it does highlight the vulnerable status of Cape Gannets at these colonies.

The conservation objective, especially for vulnerable and declining populations, should be to minimise mortality, especially of adult birds. This can be achieved by firstly reducing the frequency of oil spill events, and secondly by de-oiling birds that become contaminated, thereby mitigating the effects of oil pollution on Cape Gannet populations. Encouragingly, the release rate for oiled gannets admitted to SANCCOB between 2000 and 2005 was 88%, similar to the release rate of 86% for de-oiled African Penguins (Parsons & Underhill 2005, SANCCOB unpubl. data), and the estimated survival rates of de-oiled birds are only slightly lower than those of un-oiled birds (Altwegg *et al.*

submitted). The impact of oil contamination (and de-oiling) on the reproductive success of Cape Gannets has not been investigated, and thus remains a priority research topic that should be pursued following future oil spill events.

REHABILITATION AND RESTORATION OF DE-OILED AFRICAN PENGUINS

The sinking of the *Apollo Sea* heralded a phase of renewed penguin oiling, largely the result of fuel oils spilt from stricken cargo vessels. The *Apollo Sea*, a bulk ore carrier, broke up and sank at 33°32'S, 17°50'E, near Dassen Island off the south-western coast of South Africa, on 20 June 1994 releasing some 2 400 tonnes of heavy fuel oil (Erasmus 1995). The oil drifted first north past Dassen Island and then was rapidly wind driven south-eastwards, passing Robben Island before being coming ashore on the mainland coast near Cape Town. No emergency message was sent from the stricken vessel and the first indications of the disaster were oiled penguins coming ashore at Dassen Island.

A massive oiled seabird rescue operation was launched, involving the South African National Defence Force, Western Cape Nature Conservation Board (the provincial conservation authority) and hundreds of volunteers. In all 9 758 oiled penguins were caught and transferred to SANCCOB's seabird rescue centre outside Cape Town. The majority of penguins were from Dassen Island (about 7 200) and Robben Island (2 400). Smaller numbers of penguins were collected from Vondeling Island (about 50), islands in Saldanha Bay (about 86) and from other localities (Crawford 1994, 1995, Dehrmann 1994). The overwhelming number of birds led to a collapse in admissions procedure and records kept cannot tie individual birds to their source locality. Facilities at SANCCOB's rescue centre were inadequate to handle the unusually large number of birds, so satellite facilities to hold cleaned birds were set up at a nearby military bases. Description of, and comment on, the capture, transport and treatment of oiled penguins during this spill are provided by Barrett *et al.* (1995).

Six years later, almost to the day, another bulk ore carrier, the *Treasure*, broke free while being towed out to sea from Table Bay and sank between Robben and Dassen Islands on 23 June 2000 (Cheney 2000, Kuyper & Williams 2004). It had about 1 500 tonnes of

heavy fuel on board, most of which spilt into the surrounding sea (Crawford *et al.* 2000b). Oil started coming ashore on Robben Island on 24 June, and later moved northwards towards Dassen Island, which it reached on 28 June (Crawford *et al.* 2000b). Thousands of oiled penguins started coming ashore within days of the spill, mostly at Robben Island, and by the time the spill had been cleaned over 19 000 oiled penguins had been caught and sent to SANCCOB. As was the case during the *Apollo Sea* spill, the facilities at SANCCOB were insufficient to manage the large numbers of contaminated birds. A temporary stabilisation and bird care facility was therefore established at Salt River, in Cape Town. The majority (82%) of the oiled birds were kept at Salt River; the remainder were stabilised and de-oiled at the SANCCOB facility at Tableview (Crawford *et al.* 2000b).

Nest counts of penguin populations at Robben and Dassen Islands have been conducted annually since 1983 and 1987, respectively (Underhill *et al.* 2006). This permitted assessment of the effects of these spills on the respective populations. Soon after the release of de-oiled survivors of the *Apollo Sea* spill (most of which were fitted with flipper-bands), various studies were initiated to determine the conservation value of the rescue and de-oiling interventions (e.g. Underhill *et al.* 1997, 1999, Whittington 1999b, 2002, this thesis). Much of this work was continued following the *Treasure* spill (e.g. Hemming 2001, Barham *et al.* 2006, 2007, submitted, this thesis). In addition post-release monitoring of de-oiled penguins from a spill of unknown origin near Dyer Island (34°41'S, 19°25'E) in 1995, and from a pipeline spill at Cape Town Harbour in 1998, was conducted from 1995–1999 (Whittington 2000, 2002). These data provide the basis for the following account.

SPILL-INDUCED MORTALITY

A severe problem in assessing the effects of oil spills upon seabird populations is determination of the overall number of birds that die as a result, directly or indirectly, of the spill (e.g. Ford *et al.* 1987, Piatt *et al.* 1991, Burger 1992). Opinions vary on what proportions of birds affected are subsequently found, on the fate of de-oiled birds in the period immediately after release back into the wild, and, in the case of oiling during breeding, of the effect on eggs and chicks of the removal of parents. The *Apollo Sea* and

Treasure spills provide well documented evidence of mortality in three major phases of the spill. These are: immediate (pre-rescue) mortality; mortality between capture and release; and the mortality of eggs and chicks as a result of removal of oiled adults.

Immediate mortality

Immediate mortality of oiled birds is difficult to determine because, if birds die at sea, only a proportion are washed ashore and found (e.g. Bibby & Lloyd 1977, Page *et al.* 1990, Piatt *et al.* 1990, 1991), especially if the pollution occurs far offshore (Wilhelm *et al.* 2007). Carcasses may sink at sea or be carried away from shore by winds or currents, and beached carcasses may be covered by sand or removed by scavengers (reviewed by Burger & Fry 1993). Penguin carcasses that are beached tend to persist for a maximum of two months (Gandini *et al.* 1994).

During the *Apollo Sea* spill the prevailing winds were on-shore, so the majority of oiled penguins which died at sea should have been washed ashore. Searches on mainland beaches during and immediately following (one month) the spill period located only two oiled carcasses compared with 12 un-oiled carcasses of penguins that had died of other causes (Underhill *et al.* 1999). Few oiled penguins were found dead at the islands (A.J. Williams pers. comm.). No oiled penguins were found dead at or near Dyer Island following the unknown oil spill there in 1995 (Whittington 2002), or after the Cape Town Harbour spill in 1998 (Whittington 2000). Approximately 150 of the more than 19 000 penguins that were oiled following the *Treasure* oil spill were estimated to have died in the wild (Crawford *et al.* 2000b). At Dassen Island, despite extensive searches for oiled penguins during the *Treasure* rescue operation, no oiled birds were found dead, although 14 out of the 3 530 oiled birds that were caught alive at Dassen Island died before they could be sent to SANCCOB (Chapter Six). This evidence indicates that most oiled African Penguins manage to get ashore alive, and that the numbers of oiled birds that are observed and caught provide a reasonable reflection of the total number of birds affected. The evidence from these and previous spills also indicates that African Penguins return to shore even if contaminated by only a small amount of oil (Cooper 1972, Morant *et al.* 1981, Underhill *et al.* 1999).

Mortality between capture and release

Most penguin deaths during the *Apollo Sea* spill occurred when the penguins were under human care. Of the approximately 10 000 penguins caught for treatment, 5 200 died (Williams 1995). Of these 1 800 penguins were dead on arrival at SANCCOB's rescue station. This is 35% of all the birds that died and 18% of all the penguins captured. Many of these birds probably died through suffocation during transport as a result of the use of non-ventilated containers (for example cardboard boxes), and under-supervised packers attempting to load as many boxes of birds as possible onto transport to SANCCOB. A further 1 000 penguins died within 24 hours of arrival at SANCCOB. Altogether 54% of all deaths occurred within the first 48 hours of captivity (Williams 1995). This is a time of extreme stress for the birds and is when the weakest birds die. Most of the remaining 2 400 penguin deaths while in human care were from stress-related diseases (SANCCOB unpubl. data). Despite the lamentably high level of mortality after capture, about 4 800 penguins were de-oiled and released (Underhill *et al.* 1999). Had there been no rescue and de-oiling then almost 10 000 oiled penguins, more than 5% of the world population at the time (Crawford *et al.* 1995b), would probably have died of starvation, dehydration or as a result of acute toxicity following the ingestion of oil (Rosie & Barnes 1983, Kerley & Erasmus 1987, Khan & Ryan 1991, Jessup & Leighton 1996).

Due mostly to better preparedness by SANCCOB and conservation authorities for oil spill events after the *Apollo Sea* spill (Chapter Six), the mortality of penguins between capture and final release was substantially reduced after 1995 (Figure 7.2). Whereas 48% of the oiled penguins collected after the *Apollo Sea* spill were successfully released, more than 90% of the 19 000 oiled penguins collected after the *Treasure* spill were released back into the wild (Crawford *et al.* 2000b). This improved release rate has been sustained in the five years following the *Treasure* spill (Parsons & Underhill 2005, Figure 7.2)

Mortality of eggs and chicks

The removal of oiled adult penguins from islands disrupts breeding attempts and many eggs and chicks become deserted as a result (Underhill *et al.* 1999, Crawford *et al.* 2000b, Chapter Six). This is not only due to the breeding adults being removed from their nests, but also due to the high level of disturbance associated with rescuing oiled birds (Shannon & Crawford 1999). It is difficult to estimate the number of eggs that are

lost due to oiling and rescue operations, but it is possible to estimate the number of chicks that would have died.

At Robben Island 38 monitored nests were occupied on 15 June 1994, five days before the *Apollo Sea* sank (M.C.M. unpubl. data). When next checked, on 12 July, 26 nests were still occupied. The overall loss of chicks at the 38 nests amounted to 23, five that were in their final pre-fledging stage and 18 that were still downy (M.C.M. unpubl. data). Therefore, there was a mean loss of 0.6 chicks per nest. There were 2 155 active nests immediately before the oil spill, so the loss of chicks at Robben Island as a result of the spill was about 1 680. However, not all these chicks would have fledged.

An alternative method of calculating chick loss at Robben Island is to assume that two out of every 3.2 birds collected were breeding (Crawford & Boonstra 1994), i.e. that 1 500 of the c. 2 400 birds collected at the island were breeding. If each represented a different nest and each nest were to have fledged 0.47 chicks, the mean observed at Robben Island between 1989 and 1995 (Crawford *et al.* 1999b), the overall loss of fledged chicks for the breeding season during and following the spill would have been 705. The large discrepancy between the two estimates relates to the impact of disturbance on birds that were not oiled. It is important to note that this figure represents the number of chicks lost as a direct result of the oil spill, and does not reflect the remaining lifetime reproductive output of these birds.

Applying this latter procedure to Dassen Island, the estimated number of breeding adults oiled following the *Apollo Sea* spill is 4 500, which might have been expected to fledge 2 115 chicks in the year of the spill. This is likely to be an underestimate because the mean reproductive output for penguins at Dassen Island for the period 1994–1999 (0.89 chicks fledged per pair per attempt or 1.13 chicks fledged per year, Chapter Five) was substantially greater than the mean figure used above for birds at Robben Island. However, using the conservative estimate from Robben Island, and assuming that annual survival is 50% in the first year and 83% subsequently (mid-point values of survival figures reported for the species, Hockey *et al.* (2005) and references therein), and that the mean age at first breeding is four years (Whittington *et al.* 2005c), the loss of chicks at Dassen and Robben Islands in the year of the spill equates to a loss of

about 806 potential future breeders. This simple model serves to illustrate that one-time losses during the breeding season carry over into subsequent years.

Following the *Treasure* oil spill, an estimated 4 000 penguin chicks died at Robben and Dassen Islands (Crawford *et al.* 2000b), 43% more than the chick mortality from the *Apollo Sea* spill. These losses, together with the contamination of over 19 000 penguins and the massive disturbance at Robben and Dassen Islands caused by the rescue operation, were predicted to lead to reduced recruitment of breeders to colonies, especially Robben and Dassen Islands, after the spill (Crawford *et al.* 2000b).

Impacts on island populations

The potential overall mortality of penguins from the *Apollo Sea* spill was of the order of 13 000 adults, juveniles and fledged chicks. If the overall mortality rate of penguins during captivity were applicable to birds from all source localities, some 3 744 penguins from Dassen Island and 1 248 from Robben Island would have died. Annual counts of the number of active nests at these islands have been conducted since the late 1980s (Crawford *et al.* 1995b, c, Chapter Four). At Robben Island estimates of the overall number of penguins present are available from counts every two weeks of birds in the feather-shedding stage of moult (Randall *et al.* 1986, Crawford & Boonstra 1994, Crawford *et al.* 1995c, 1999b). Moult counts have been conducted at Dassen Island since November 1994, but are less useful as estimates of the overall penguin population (see Chapter Four).

At Dassen Island 9 389 active nests (those nests with eggs, chicks, or defending adults present) were counted between 8 and 13 April 1994, two months before the *Apollo Sea* sank. In 1995 9 792 active nests were counted in the period 6–10 April, and in 1996 9 502 nests between 17 and 24 March (Underhill *et al.* 2006, M.C.M. unpubl. data). These counts indicate no substantial change in the overall breeding population at Dassen Island in spite of the probable death of 4 160 oiled penguins from this locality. Counts by sub-areas suggest the loss of 3 200 adults from regions adjacent to where oil came ashore. These losses were offset by increases elsewhere on the island, believed attributable to increased recruitment of new breeders and an above average proportion of the adult population that attempted breeding (Crawford *et al.* 1997) due to above average food availability. It is also possible that the disturbance during the rescue

operation may have caused some birds to relocate nest sites to other areas on the island. Due to the paucity of re-sighting data prior to the spill, it was not possible to determine whether this was a factor.

At Robben Island, the count of moulting adult birds decreased by almost 900 between 1993, prior to the sinking of the *Apollo Sea*, and 1995 (Crawford *et al.* 1999b). Because mean duration of the feather shedding stage of moult of African Penguins is 12.7 days (Randall *et al.* 1986) but counts were made every fourteenth day, this represents an actual loss of about 1000 adults. The number of active nests at Robben Island decreased by 520, from 2 799 counted between 30 May and 1 June 1994, prior to the spill, to 2 279 recorded between from 29 to 31 May 1995 (Underhill *et al.* 2006, M.C.M. unpubl. data). Multiplying by a factor of 3.2, which was derived to obtain an estimate of the total population from nest counts on the basis of the mean ratio of the total moult count for a year and the maximum nest count of the preceding breeding season (Crawford & Boonstra 1994), this represents the loss of 1 664 birds. These two estimates are in broad agreement with the estimated death from oiling of approximately 1 200 birds from Robben Island. In 1996, 3 097 active nests were recorded between 22 and 24 May, more than in 1994. Therefore, as with Dassen Island, good recruitment seems to have maintained the breeding population at levels similar to those before the *Apollo Sea* spill.

The African Penguin colonies at Dassen and Robben Islands continued to increase between 1995 and 2000, matching the growth in biomass of the South African stock of Sardine and Anchovy *Engraulis encrasicolus* (Barange *et al.* 1999, 2004, Crawford *et al.* 2006, in prep., Underhill *et al.* 2006). The breeding census at Dassen Island from 22–27 April 2000 (about two months prior to the *Treasure* spill) recorded 17 042 breeding pairs. This represented the highest nest count of penguins at Dassen Island between 1978, when direct counts were first undertaken (Shelton *et al.* 1984, Crawford *et al.* 1995b), and 2000 (Underhill *et al.* 2006). Similarly, the nest count of penguins at Robben Island between 17 May and 14 June 2000, was the largest number of breeding pairs (5 705) ever recorded there up to that time (Underhill *et al.* 2006). Despite the loss of at least 2 000 adult penguins from oiling, and the substantial disturbance that these colonies were exposed to at the height of the 2000 breeding season, the penguin breeding populations at Dassen and Robben Islands increased by 25% and 18%, respectively,

between 2000 and 2001 (Wolfaardt *et al.* 2001, Chapter Six). All of the penguin colonies on islands in Saldanha Bay had larger numbers of breeding pairs in 2001 compared with 2000, and there was an overall increase for Western Cape colonies north of Table Bay of 18% (Wolfaardt *et al.* 2001). This increase was attributed to an abundance of food for penguins in 2001 (Wolfaardt *et al.* 2001). The combined spawner biomass of Anchovy and Sardine in 2001 was double any previous estimate obtained by means of a direct survey (van der Lingen *et al.* 2001, Wolfaardt *et al.* 2001).

The increased breeding populations of African Penguins observed following both the *Apollo Sea* and *Treasure* spills does not mean that the oil spills had no population level impacts. The anticipated negative impacts of these oil spills were offset by the vastly improved availability of prey. Furthermore, these increases represent a partial recovery of populations that incurred substantial losses during the 20th century (Frost *et al.* 1976, Crawford *et al.* 1990, 2001). The potential recovery rates of the oil-affected colonies would have been greater in the absence of oil induced mortality. The rate of growth of these colonies following the improved feeding conditions illustrates how quickly seabird populations can respond to changes in their environment. This is again illustrated, in the opposite direction, by the 45% decline in the Western Cape penguin breeding population between 2004 and 2006 (Crawford *et al.* in prep., Chapters Four & Six), in response to a decreased biomass of Anchovy and Sardine (Barange *et al.* 2004) and an eastward shift in the distribution of this prey after 2002 (van der Lingen *et al.* 2005, Fairweather *et al.* 2006).

It is important to note that most African Penguins that have been oiled are adult birds. About 90% of the birds that were released following the *Apollo Sea* were adults (Chapter Two) and 78% of the oiled birds collected at Dassen Island following the *Treasure* oil spill were adult birds (Chapter Six). For a species which only starts reproducing from the age of four (Whittington *et al.* 2005c), and has a relatively low reproductive rate (Hockey *et al.* 2005), losses of adults from the breeding population have far more severe demographic impacts than losses of juveniles or chicks. Populations can be rebuilt only from new (or improved) reproduction or immigration from other colonies. The recovery (and increase) of the affected populations following the *Apollo Sea* and *Treasure* spills was facilitated by increased recruitment and an increased proportion of the adult population attempting to breed during a period of substantially improved feeding

conditions (Wolfaardt *et al.* 2001, Crawford *et al.* 2006, in prep.). The increased recruitment may have included the immigration of first-time breeders from other colonies, but not of established breeders, which have seldom been recorded emigrating from breeding colonies (Crawford 1998, Whittington *et al.* 2005a). Had either of these oil spills taken place during the period 2004–2006 during which populations declined, the impact of the oil mortality would have been largely additional to the other sources of mortality, such as scarcity of food, and thus far more severe. Moreover, unlike most other sources of mortality, oil contamination does not discriminate between "fit" and "unfit" individuals.

REHABILITATION

The success of de-oiling and treating contaminated seabirds has often been measured solely by the proportion of birds released back into the wild in seemingly healthy condition, normally based on body mass and behaviour (Holcomb 1991, Monahan & Maki 1991, Newman *et al.* 2003). From a population and conservation perspective, it is clearly important to determine the long-term survival and breeding productivity of de-oiled birds. Post-release studies of murres in Europe and North America in the 1980s and early 1990s showed that de-oiled birds had short survival times (generally less than 30 days) following release, and hardly any birds survived beyond the first year (Sharp 1996, Camphuysen *et al.* 1997, Wernham *et al.* 1997). Negligible survival of de-oiled individuals has led some conservation biologists to challenge the conservation value of de-oiling contaminated seabirds (Boersma 1995, Sharp 1996, Estes 1998). Despite the doubt expressed by Frost *et. al.* (1976), de-oiled African Penguins have often been cited as the species with the highest post-release survival rates (Bourne 1980, Randall *et al.* 1980, Morant *et al.* 1981, Boersma 1995, Sharp 1996), although the contribution, in conservation terms, of these earlier efforts has also been questioned (Fry *et al.* 1986, Nisbet 1994, Boersma 1995).

De-oiled birds are considered rehabilitated if they survive for a substantial period after release back into the wild. Unfit birds would be expected to die soon after release. In practice, de-oiled birds have generally been regarded as rehabilitated if they are known to have survived longer than a month after release (Goldsworthy *et al.* 2000b, Newman *et al.* 2004, Barham *et al.* 2006). However, for long-lived seabirds, it is clearly important

also to assess the longer-term survival of de-oiled birds following release. The scope of de-oiling studies has shifted to focus mostly on the biological or conservation value of de-oiling. As a result, the number of post-release studies has increased substantially in the last decade; however, few of these studies have extended beyond a year or two (e.g. Anderson *et al.* 1996, Giese *et al.* 2000, Goldsworthy *et al.* 2000b, Golightly *et al.* 2002, Newman *et al.* 2004). The South African post-release studies of de-oiled penguins and gannets are among the few exceptions.

Post-release mortality

Based on the recovery of banded birds in North America, Sharp (1996) considered that the median survival period of de-oiled seabirds was less than 10 days after their return to the wild. Other studies have also shown that the most critical period for survival occurs within the first couple of months following release (e.g. Newman *et al.* 2004), and that few de-oiled birds survive the first year following release (Camphuysen *et al.* 1997, Wernham *et al.* 1997). After the *Apollo Sea* oil spill a total of 4 076 de-oiled penguins were released with flipper bands (Underhill *et al.* 1999). A few birds returned to release-beaches within 24 hours, presumably because they were inadequately waterproofed. These birds were captured, re-washed, and released again later.

Three lines of evidence suggest that mortality of penguins in the immediate post-release period following the *Apollo Sea* spill was minimal (Underhill *et al.* 1999): 1) surveys of the coast adjacent to the main release site failed to produce carcasses of dead birds; 2) the number of banded birds found dead and reported by members of the public was consistent with what would be expected as a result of normal mortality rates; 3) approximately 45% of the released adult penguins were re-sighted alive at breeding localities within the first year of their release (Whittington 2002). As with the *Apollo Sea* spill, there was no evidence of large scale mortality following the release of de-oiled penguins from subsequent spills (Whittington 2000, 2002, Barham *et al.* 2006, Chapter Six).

The number of de-oiled penguins with flipper-bands recovered dead between 1994 and 2006 is similar to what one would expect from an equivalent sized sample of non-oiled penguins (Whittington 2002, SAFRING unpubl. data). In contrast to the results reported by Sharp (1996) for three species of North American seabird, the median time elapsed

between release and death for both de-oiled and un-oiled African Penguins was 23 months (Whittington 1999a).

Re-sighting and survival rates of de-oiled penguins

Over a five-year period, from August 1994 to July 1999, a total of 73% of the 4 076 de-oiled penguins released with flipper bands following the *Apollo Sea* spill, were re-sighted at penguin colonies; the majority (90%) of these were re-sighted at Dassen Island (Whittington 2002). The proportion of de-oiled birds that were re-sighted four years after their release following the oiling incident near Dyer Island in August 1995 was 40% (Whittington 2002), substantially lower than the figures for the *Apollo Sea* spill and all subsequent spills. One year after the Cape Town Harbour spill of 1998, 50% of the de-oiled penguins had been re-sighted at breeding colonies (Whittington 2000, 2002). Between July 2000 and December 2004, 67% of the de-oiled adult penguins from the *Treasure* spill estimated to have been from Robben Island had been re-sighted there (Barham *et al.* 2006). The most likely reason for the lower proportion of de-oiled birds re-sighted after the Dyer Island spill most likely related to the lower intensity of re-sighting effort at Dyer Island, relative to Dassen and Robben Islands (Whittington 2002). It could also have been a consequence of increased predation pressure from Cape Fur Seals (Marks *et al.* 1997) and White Sharks *Carcharodon carcharias* (Johnson *et al.* 2006) at Dyer Island, or to differences in the impacts of oil contamination between spills. The intensity of re-sighting effort, which has been variable both spatially and temporally, is a critical factor in the interpretation of re-sighting data. The relatively low re-sighting rates of de-oiled African Penguins in the 1970s and 1980s (Morant *et al.* 1981) were almost certainly influenced by the low intensity, and short-term nature, of the search effort. It has also been suggested that between-spill differences in the performance of de-oiled birds may reflect differences in the chemical properties and toxicological effects of the different oils (Barham *et al.* 2007), although this has not been explicitly tested. In order to make comparisons between different spills, it is important that the calculation of survival estimates account for differences in re-sighting effort and recapture probabilities. This can be achieved through the use of multi-state capture-mark-recapture (CMR) models (Lebreton *et al.* 1992, Pradel *et al.* 1997), such as those in the programme MARK (White & Burnham 1999).

The patterns of cumulative re-sightings of de-oiled penguins were similar after each of these spills, showing a rapid increase during the first year following release, after which the rate started levelling off (Whittington 2002, 2003, Barham *et al.* 2006). A minimum of 37% and 35% of de-oiled penguins re-sighted after the *Apollo Sea* and Dyer Island spills, respectively, were still being observed five years after their release (Whittington 2002), indicating that a large proportion of the rehabilitated birds survived considerable periods of time after de-oiling. This observation is further supported by the finding that that, for the period 1990–1999, the average annual survival rate of non-oiled (control) adult African Penguins at Robben and Dassen Islands (0.81) was similar to that of de-oiled adult African Penguins (0.79) over the same time period (Whittington 2002). Five penguins de-oiled by SANCCOB have subsequently survived for between 20 and 25 years, including two of the three oldest African Penguins on record (Whittington 1999a, Whittington *et al.* 2000a). These, I believe, are the longest periods of post-oiling survival for any seabirds.

The proportions of de-oiled juvenile African Penguins re-sighted after release were less than those of adults (Whittington 2002, 2003, Barham *et al.* 2006, Chapters Two and Six). The annual survival rate of juvenile birds is less than that of adults (Randall 1983, La Cock *et al.* 1987, La Cock & Hänel 1987, Whittington 2002), and so the re-sighting rate (and survival) of de-oiled birds would be expected to be lower than for adult birds. In addition, juvenile penguins disperse up to 1 900km from their natal island during their first year (Randall *et al.* 1987, Whittington 2002, Whittington *et al.* 2005b), so it is possible that many of the juveniles that became oiled during spills in the Western Cape, were actually from colonies outside of this region. The return of these birds to their natal colonies (outside of the region) following release would reduce the probability of their being re-sighted, especially if the natal colonies were subject to less intensive monitoring than the colonies in the Western Cape, where the majority of de-oiled adults have been re-sighted (Whittington 2002).

The population-level benefits of de-oiling African Penguins

The contribution that de-oiling has made to the current population of African Penguins is significant and measurable. Using a deterministic, age-structured model of the African Penguin population, Ryan (2003) estimated that the global population of African

Penguins was 19% larger (33 000 birds) in 2002 than it would have been if de-oiling had not taken place since the establishment of SANCCOB in 1968.

In addition, Ryan (2003) used a stochastic model to estimate the future benefits of continued de-oiling in the face of catastrophic spills and chronic oiling of different intensities and frequencies. Although catastrophic spills, which typically occur close to breeding colonies, result in much larger numbers of penguins becoming contaminated, the long-term cumulative impact of ongoing low-level oiling may be as severe as a once-off catastrophic event for the conservation of African Penguins (Shannon & Crawford 1999). Chronic oil pollution is a significant mortality factor for Magellanic Penguins *Spheniscus magellanicus* and results in the death of at least 40 000 penguins along the Argentine and Brazilian coastlines each year (Perkins 1983, Boersma 1987, Gandini *et al.* 1994, García Borboroglu *et al.* 2006). Chronic oiling has resulted in the contamination of an average of 600 African Penguins per year; after 1990 the average number of birds affected by chronic oiling increased to 925 birds per year (Ryan 2003, Parsons & Underhill 2005, Figure 7.1).

The stochastic model used by Ryan (2003) predicted that, in the absence of catastrophic spills, de-oiling birds affected by chronic oiling alone would result in a 7% larger population after 20 years than if no de-oiling took place. Assuming that a catastrophic spill kills 5% of the population (without de-oiling), the percentage increase in the mean projected population after 20 years resulting from de-oiling ranged from 14–33%, as the probability of a spill increased from 5–20% per year. If catastrophic spills kill 10% of the population (the *Treasure* spill oiled 12% of the global population at the time, but threatened at least 25% of the population), the projected benefits of continued de-oiling ranged from 15–61% after 20 years, as the probability of spills increased from 2.5% to 20% per year (Ryan 2003).

Orphans

A novel aspect of the *Apollo Sea* spill was the collection, and rearing, of orphaned chicks (Gildenhuys 1995, Whittington & Gildenhuys submitted). The removal of large numbers of oiled, adult penguins from Dassen and Robben Islands left many chicks orphaned in the nest. Early in the rescue operation it was decided that efforts would focus on oiled adult birds, as these would have the greatest chance of survival and were more likely to

breed in the future. However, after the removal of all oiled, adult penguins, staff at the islands collected many large chicks for hand-rearing. At Robben Island, 551 chicks were collected and transferred to the Cape Town where 508 were raised to "fledging". These birds were not banded and their fate after release is unknown. On Dassen Island, 507 chicks aged (by plumage development) 30 days or older were collected, housed under shelter on Dassen Island, and hand fed. Access to the sea was provided at night and 474 of the chicks, 437 of which were flipper-banded, fledged at their own pace (Gildenhuys 1995, Whittington & Gildenhuys submitted). Some subsequently travelled to Namibia (Underhill *et al.* 1999). From August 1994 to June 1999, 47 (10.8%) of the hand-reared chicks with flipper bands were re-sighted, similar to the proportion (9.0%) of 399 naturally fledged chicks flipper-banded at nest sites on Dassen Island in 1994 that were re-sighted during the same time period (Whittington & Gildenhuys submitted). The patterns of dispersal of these two groups following banding were similar, as were the proportions that were recorded breeding (15% of the re-sighted birds from both groups), and the mean age of first recorded breeding (Whittington & Gildenhuys submitted).

Fifty orphaned chicks were hand-reared on Dyer Island following the oiling incident that took place there in August 1995 (Table 7.3). The proportion (18%) of these birds that were re-sighted over a three year period, from October 1996 to October 1999, was larger than the proportion re-sighted following the *Apollo Sea* spill (Whittington & Gildenhuys submitted). None of the 50 hand-reared orphans was recorded breeding by October 1999 at Dyer Island; one of the birds re-sighted was recorded breeding away from its natal colony, at Boulders Beach (34°11'S, 18°27'E) (Whittington & Gildenhuys submitted).

On the basis of these findings, an effort was made to collect and hand-rear chicks that were abandoned on Robben and Dassen Islands following the *Treasure* spill in June 2000 (Crawford *et al.* 2000b, Barham *et al.* submitted, Chapter Six). As was the case in the *Apollo Sea* seabird rescue operation, the collection of orphaned chicks was initiated after most of the adult birds had been collected for de-oiling or to be evacuated (Crawford *et al.* 2000b, Wolfaardt 2004, Barham *et al.* submitted, Chapter Six). A total of 3 350 orphaned chicks were collected, 2 643 from Robben Island and 707 from Dassen Island (Crawford *et al.* 2000b, Barham *et al.* submitted, Chapter Six). In total, 1 787 were released with flipper-bands, 732 on Dassen Island, and 1 055 on Robben Island

(Barham *et al.* submitted, Chapter Six). The birds released on Dassen Island were reared at Monty's rehabilitation centre near Melkbosstrand (33°43'S, 18°26'E); those released on Robben Island were reared at SANCCOB and its satellite centres (Chapter Six). The orphaned chicks were not kept separate after collection from these two islands, and so the natal colony of the released chicks was unknown. About 33% of the released birds were re-sighted between 2001 and 2006 at Robben and Dassen Islands (Chapter Six), treble the proportion of hand-reared chicks released after the *Apollo Sea* spill, over a similar period. Approximately 10% of the hand-reared chicks re-sighted were observed at both Dassen and Robben Islands (Chapter Six). It is noteworthy that, at both islands, a significantly lower proportion of the chicks reared at the Monty's facility were re-sighted, compared with those released from SANCCOB. This difference in re-sighting rate (and survival) is thought to have been influenced by the much higher release masses of chicks from the Monty's centre, which may have impaired their manoeuvrability in the water and thus their ability to escape predators (Chapter Six).

The differences in the proportions of hand-reared orphans re-sighted from the different cohorts is consistent with the variable survival rates of naturally-fledged first year birds (Randall 1983, La Cock *et al.* 1987, La Cock & Hänel 1987, Whittington 2002), and probably reflects changes in the distribution and abundance of their dominant prey. Variable re-sighting effort has probably also contributed towards differences in re-sighting rates between cohorts.

The proportion (34%) of re-sighted hand-reared chicks from the *Treasure* spill that were recorded breeding between 2002 and 2006 at Robben Island was substantially greater than has been recorded from previous cohorts (Barham *et al.* submitted, Whittington & Gildenhuys submitted). It was also greater than the proportion of *Treasure* orphans recorded breeding at Dassen Island (Chapter Six). The larger proportion of birds recorded breeding at Robben Island was likely the result of a greater intensity of re-sighting effort at Robben Island from 2001 to 2006 than at Dassen Island during this period (Chapter Six), and compared with the monitoring of previous cohorts. Once they have reached breeding age, hand-reared chicks appear to be able to breed as successfully as naturally-reared chicks. Over a four year period (2002–2006) at Robben Island, the breeding success of pairs where at least one member was a hand-reared

Treasure orphan, was at least as good as pairs where both members were naturally reared, and had never been oiled (Barham *et al.* submitted).

RESTORATION OF DE-OILED BIRDS

In conservation terms rehabilitation, even if the rehabilitated bird survives for months or years, is of little relevance unless the bird is restored into the productive breeding population of the species. The conservation aim is that the bird will breed successfully and, ideally, at the same rate and with the same expectation of success as control individuals. Ongoing, follow-up studies of African Penguins de-oiled after the spill provide the world's best indication of whether such post-oiling restoration occurs.

Proportion of de-oiled penguins recorded breeding

De-oiled African Penguins have been monitored sporadically since the 1970s (Randall *et al.* 1980, Morant *et al.* 1981). The proportion of re-sighted de-oiled penguins observed breeding following seven separate oil spills between 1970 and 1979 ranged from 0% to 30%, with an average of 20% (Morant *et al.* 1981). These figures have generally been regarded as the highest rates of survival to reproduction for de-oiled seabirds (Morant *et al.* 1981, Boersma 1995, Sharp 1996), but have also been interpreted as indicating reduced long-term performance of de-oiled birds by some authors (Fry *et al.* 1986, Fry & Addiego 1987, Nisbet 1994). These earlier studies of de-oiled African Penguins were generally of an opportunistic nature, and limited in terms of the intensity and duration of the re-sighting effort.

The more intensive and longer-term monitoring of de-oiled penguins from the *Apollo Sea* spill (this thesis), which also involved a much larger sample size, showed that approximately 74% of the adult penguins that were re-sighted in a intensively-monitored study area on Dassen Island were recorded breeding over a period of 10.5 years (Chapter Two). Conversely, about 26% of the de-oiled penguins re-sighted never attempted breeding after their release from SANCCOB, even though some of these birds were still being regularly observed towards the end of the study period, more than 10 years after release.

Although some de-oiled individuals resumed breeding almost immediately following the *Apollo Sea* spill (Underhill *et al.* 1999), for most penguins which were eventually recorded breeding, there was a delay between their first re-sighting and first recorded breeding attempt (median interval = 11 months, Chapter Two). Similarly, de-oiled adult penguins from the *Treasure* spill were restored at a slower rate than un-oiled adult penguins which were evacuated (Chapter Six).

Although the improved restoration results obtained in the *Apollo Sea* and *Treasure* follow up studies, compared with those which took place in the 1970s (Cooper 1972, Randall *et al.* 1980, Morant *et al.* 1981), were most likely due to the greater intensity and duration of re-sighting effort, better stabilisation and treatment of oiled penguins may also have contributed towards the improved restoration rates. The rate at which oiled birds have been successfully released after de-oiling has steadily increased between 1970 and 2006 (Randall *et al.* 1980, Morant *et al.* 1981, Nel *et al.* 2003, Parsons & Underhill 2005, this chapter). The improved release rate is more likely to be due to advances and better organisation in the capture, stabilisation and the veterinary bird care components of oiled seabird rescue than the actual de-oiling (cleaning) methods, which have remained relatively unchanged over the last few decades (A.J. Williams pers. comm.).

Breeding success and chick growth rates

The effect of oiling and de-oiling on subsequent breeding ability of African Penguins in the *Apollo Sea* spill was studied by comparing breeding success parameters of nests which comprised either one or two de-oiled birds with those in which none of the birds had been oiled (control nests); 18 separate studies were conducted over a six year period (Chapter Five). Overall, the fledging success of *Apollo Sea* nests was significantly lower than that of control nests (reduced by about 11%). The reduced productivity was greater for nests in which both partners were de-oiled birds, and during studies in which the breeding success of all nests was relatively low (relative to the mean for the six years).

The breeding success of de-oiled African Penguins from the *Treasure* oil spill was also lower than that of un-oiled penguins. From 2001 to 2005, the fledging success of de-oiled *Treasure* penguins at Robben Island was an average of 18% lower than penguins that had never been oiled (Barham *et al.* 2007). The greater margin of difference

between de-oiled and un-oiled birds observed in the *Treasure* group (compared with *Apollo Sea* birds), highlights the fact that spills are not identical, and thus the difficulty (and risk) of extrapolating results from one oil spill to others. Possible reasons for the differences in the relative breeding performance of de-oiled penguins from the *Apollo Sea* and *Treasure* spills include differences in the chemical properties (and toxicity) of the oil, the extent of oiling per bird, the body condition of oiled birds when captured, the interval between capture and de-oiling, and the interval between capture and release (Morant *et al.* 1981, Kerley & Erasmus 1987, Barham *et al.* 2007).

The growth rates of chicks which were reared by pairs with one de-oiled *Apollo Sea* parent were similar to those raised in control nests. However, chicks raised by pairs comprising two de-oiled birds had significantly lower growth rates than chicks raised in control nests. As with the fledging success results, these differences were greater in studies in which growth rates were reduced relative to the mean for the entire study period (1994–1998) (Chapter Five).

The patterns of chick mortality for *Apollo Sea* and control nests differed. A greater proportion of chicks from *Apollo Sea* nests died when they were older than 40 days (Chapter Five), which is generally the most energetically demanding period of growth, when chicks are most susceptible to dying of starvation (Cooper 1977, Seddon & van Heezik 1991, van Heezik & Seddon 1991, Bouwhuis *et al.* in prep). This result, together with the reduced growth rates of chicks from nests with two de-oiled *Apollo Sea* birds, suggests that oil contamination compromised the ability of African Penguins to meet the energetic requirements of their chicks, especially at the time of peak energy demand, an effect that was not reversed through the de-oiling process. Their reduced ability to rear chicks was exacerbated when environmental conditions (probably food availability) deteriorated (inferred from overall reduction in breeding success and chick growth rates), which presumably placed additional stress on all breeding birds, but especially on de-oiled birds.

The relatively high rate at which de-oiled birds stopped breeding, and the lower survival estimates for de-oiled secondary nonbreeders (birds which abstain from breeding in a given year, but had bred previously) suggest a cost of reproduction for de-oiled birds (Chapter Two). These results also suggest that the effects of oiling may become

especially apparent when de-oiled birds become stressed, such as when they undertake the energetically demanding process of breeding, a finding that is further supported by comparing the de-oiled *Treasure* penguins with un-oiled evacuees (Chapter Six).

Possible reasons for oil effects on breeding performance

Two important questions are raised by these findings. Firstly, why are some 26% of rehabilitated birds unable to breed following de-oiling? Secondly, why do de-oiled African Penguins breed less successfully than control birds? There are a number of possible explanations, which are not necessarily incompatible.

De-oiling is focused primarily on the exterior of the bird, even though efforts are made during captivity to reduce the effects of oil ingestion. At SANCCOB two standard treatments are used that counter-act ingested oil. Birds are fed activated charcoal to absorb toxins (Parsons & Underhill 2005). Additionally birds are given electrolyte solution which, though aimed at re-hydrating the bird, also serves to flush out toxins (Dehrmann 2006). However, a "cleaned" released bird has not necessarily been unharmed internally. Experimental studies of other seabirds have shown that organs such as the liver and kidneys often suffer long-term damage after the ingestion of even minute quantities of oil (Fry & Lowenstine 1985). This damage can lead to modification or impairment of hormonal balance. In turn this may be associated with disruption of courtship, breeding, and other activities (Peakall *et al.* 1981, Fowler *et al.* 1995). After limited recovery from toxicity, there may be disruption of "normal" reproductive behaviour under physiologically stressful situations (Peakall *et al.* 1980, Butler *et al.* 1988, Eppley & Rubega 1990, Eppley 1992). Ingested oil may also irreversibly damage the reproductive organs, effectively sterilising the affected birds (Chapter Two).

Another possible cause of post-oiling reproductive failure is the disruption of bonds between members of established breeding pairs. A high degree of pair fidelity is a typical trait of seabirds (Lack 1968), and breeding success is generally greater in established pairs of several seasons standing than it is in recently formed pairs (e.g. Richdale 1957, Coulson 1966, Wood 1971, Mills 1973, Thibault 1994, Choudhury 1995, Bried & Jouventin 2002). Studies of African Penguins indicate an annual fidelity rate of between 80% and 94% under "normal" circumstances (Randall 1983, Crawford *et al.* 1995c). At Dassen Island, the fidelity rate of de-oiled *Apollo Sea* breeders between 1995 and 2000

was 65%, considerably lower than the 88% fidelity rate for un-oiled control birds over the same period (Chapter Five), and the 80–94% range reported for this species. Moreover, patterns of mate fidelity were associated with reproductive success. Penguins were more likely to separate if they had failed to raise a chick in the previous attempt, and pairs which re-united exhibited greater reproductive success than those which nested with a new mate (Chapter Five).

There are several ways in which oil spills can disrupt established pair-bonds. Mortality of one pair member forces the mate to find a new partner. Even where both partners survive an oil spill, they may be unable to re-unite. Among reasons for failure to re-unite may be subsequent asynchrony in their annual moult (Underhill & Crawford 1999, Hemming 2001, Chapters Three and Four), or differences in the time spent in captivity, or in the time required before the bird is again physiologically able to breed. The links between fidelity and reproductive success are confounded by the effects of age and experience (e.g. Ainley *et al.* 1983), and the possible impacts of oiling on bird condition, which may influence reproductive success and mate choice. The cause and effect relationships between oiling, mate fidelity and reproductive success are difficult to separate and require further investigation.

Post-release studies of other seabirds, including Little Penguins *Eudyptula minor* (Giese *et al.* 2000) and Magellanic Penguins (Fowler *et al.* 1995), have also shown reduced breeding abilities among de-oiled birds. Oil effects on breeding have also been demonstrated for mammals. Ranch-reared Mink *Mustela vison* experimentally dosed with petroleum products were found to exhibit reduced reproductive success, even though they showed no clinical symptoms of toxicosis or behavioral abnormalities (Mazet *et al.* 2001). In addition, kits of female Mink fed oil-contaminated food had reduced survival to weaning; the impacts of oil on reproductive success persisted for at least two generations, even though the only exposure of kits to petroleum was *in utero* or while suckling (Mazet *et al.* 2001).

Population-level benefits of restoration

Despite the impact of oil contamination on the breeding performance of African Penguins, the species remains the most successfully restored of any seabird following oiling (Chapter Two). Although the breeding productivity of *Apollo Sea* birds between

1994 and 2000 at Dassen Island (mean = 0.83 chicks fledged per pair per breeding attempt, or 1.05 chicks fledged per pair per year) was 11% lower than that of control birds, it was still higher than most other breeding success figures that have been reported for the species (Chapter Five). Using the figures for de-oiled *Apollo Sea* birds, of 1 000 adult females de-oiled, 27% do not breed again, and a further 31.5% of those that do breed, do not breed in any given year (Chapter Two). On the basis of a mean productivity of 1.05 chicks fledged per de-oiled female per year at Dassen Island from 1995–1999 (Chapter Five), the estimated lifetime reproductive output of these birds would be 3 088 chicks. This is based on a remarkably high breeding productivity during a period of favourable feeding conditions (Chapter Five). The mean breeding output of de-oiled *Treasure* females at Robben Island for the period 2001–2005 was 0.61 chicks per attempt (Barham *et al.* 2007). Assuming that 27% of females laid a second clutch (Crawford *et al.* 1999b, Chapter Five), the mean breeding output of de-oiled *Treasure* females would be 0.77 chicks per year. Using this lower estimate, the estimated lifetime reproductive output of these de-oiled birds would be 2 265 chicks. Clearly, de-oiled African Penguins have contributed towards the productivity of oil-affected populations, as well as mitigating many of the other threats that face this species.

Assuming an age of first breeding of four years, survival in the first year of 0.43, and 0.81 for subsequent years, Crawford *et al.* (2006) determined that it would be necessary for pairs to fledge an average of 1.66 chicks per year to maintain the population in equilibrium. This was based on the assumption that all adults of breeding age reproduce each year, which is not the case, both for un-oiled penguins (Whittington *et al.* 1996, Crawford *et al.* 1999b), and for de-oiled birds (Chapter Two). When first-year and subsequent survival is increased, the breeding output required to sustain the African Penguin population is reduced. For example, when first year survival is increased to 0.50, and adult survival to 0.85, the required annual production of chicks to maintain equilibrium is reduced to 0.96 chicks (Crawford *et al.* 2006). Based on current estimates of survival, the de-oiled birds are not producing sufficient recruits back into the breeding population. However, this is also the case for un-oiled birds (Crawford *et al.* 2006), and would be substantially worse if oiled birds were not de-oiled, but left to die (Ryan 2003). This highlights the vulnerable conservation status of the African Penguin, and the need to minimise mortality. De-oiling contaminated birds is one way to achieve this goal.

COST EFFECTIVENESS

The cost of penguin rescue and de-oiling during the *Apollo Sea* spill was 2 149 375 South African Rands (equivalent at that time to about 589 000 US Dollars) (Erasmus 1995). This was the total combined insurance claim by SANCCOB and other organizations for seabird rescue and treatment (including helicopter and ship time). This sum excludes donations of materials to SANCCOB during the crisis, and the time "donated" by volunteers working with the penguins. The cost per penguin rescued, de-oiled and released back into the wild was estimated as R412, or US$112 (Nel *et al.* 2003).

The proportion of oiled birds originating from Dassen Island was 72%. If we assume that 72% of the funds were spent on penguins from that island then the cost of each adult penguin restored to the breeding population was R855 (US$238). The cost per successfully restored penguin is greater than the cost per successfully de-oiled penguin because the total cost is spread over fewer birds (i.e. those that attempted breeding subsequent to their release). Apportioning the costs in terms of the proportion of juvenile penguins (8.5%) that were de-oiled (Chapter Two), the cost of rehabilitating each juvenile was R1 739, and the cost of each juvenile restored to the breeding population R4 350.

As the offspring of de-oiled birds recruit into the breeding population, the cost of de-oiling efforts is spread over a larger number of individuals. The predicted cost per breeding adult penguin produced as a direct result of the de-oiling efforts following the *Apollo Sea* spill will thus decrease with time. Conversely, the investment in de-oiling contaminated penguins grows with time. To maximise the investment, one needs to: 1) reduce the initial cost; 2) reduce the lag time between payment of the initial cost and the point at which the investment begins to grow; and 3) increase the rate at which the investment grows.

Reducing the initial cost can be achieved by maximising the release rates from SANCCOB as well as the post-release survival rates. It thus makes sense to prioritise de-oiling adult penguins, which have greater post-release survival rates compared with juvenile penguins or orphaned chicks. The time lag between the initial cost and when the

investment begins to return benefits can be decreased by ensuring that de-oiled birds begin breeding as soon as possible after being released. Measures that reduce the amount of time birds spend in captivity are likely to contribute towards this goal, by minimising the exposure to diseases and other potentially deleterious impacts of captive conditions (Kerley & Erasmus 1987, Parsons & Underhill 2005), and reducing disruptions to the normal annual cycle of affected birds (Underhill & Crawford 1999, Chapters Three and Four) and to pair bonds (Chapter Five). This time lag can also be reduced by prioritising adult penguins, which produce chicks that are recruited into the breeding population at least four years before juvenile penguins can. The rate at which the investment grows is governed by the rate at which adults produce recruits into the breeding population. This is in turn dependent on the breeding success of affected birds as well as first-year and subsequent survival rates. Breeding success of African Penguins is significantly influenced by the abundance and distribution of their dominant prey, Anchovy and Sardine (Adams *et al.* 1992, Crawford & Dyer 1995, Crawford *et al.* 2006, Chapter Five). First-year survival is also influenced by forage fish availability (Whittington 2002). In addition, high levels of Cape Fur Seal predation on juvenile penguins, especially along the west coast, may contribute towards reduced survival-rates of first year birds (Whittington *et al.* 2000b). Oil mortality itself also impacts survival rates for all age-classes. By managing all of these issues, the conservation value of de-oiling African Penguins can be further improved.

The insurance claim for costs incurred during the seabird rescue and de-oiling process following the *Treasure* spill was R10 166 544 (Nel *et al.* 2003), equivalent to US$1 459 000 at the time. This equates to a cost of R628 (US$90) per de-oiled individual penguin released (Nel *et al.* 2003). The reduced cost per released bird (in US Dollar terms) relative to the *Apollo Sea* spill was probably due to the higher release rate of oiled penguins that were admitted to SANCCOB following the *Treasure* spill (Nel *et al.* 2003). The evacuation of un-oiled African Penguins during the *Treasure* spill also contributed towards a reduction in the lag between the initial cost and the point at which the investment started to return benefits, and also the growth rate of the investment. This is because the evacuated birds resumed breeding much more rapidly than de-oiled birds (Chapter Six) and did not suffer any of the harmful impacts of oil contamination on breeding productivity (Barham *et al.* 2007).

The cost per bird de-oiled in a typical North American spill is estimated to be about US$5 000 (Boersma 1995). In the *Exxon Valdez* spill each de-oiled bird released cost in the region of US$10 000 (Monahan & Maki 1991). The cost for each Sea Otter *Enhydra lutris* released back to the wild was even higher, at about US$80 000 (Estes 1991). Even though there is some discrepancy about the cost accounting methods used to determine these figures (Jessup 1997, 1998), it is clear that the cost of de-oiling African Penguins is substantially less than has been reported for seabirds in the northern hemisphere.

CONCLUSIONS

Oil pollution is currently a significant threat to African Penguin and, to a lesser extent, Cape Gannet populations. It acts in combination with a number of other threats. There is evidence that substantial numbers of de-oiled Cape Gannets and African Penguins can be rehabilitated, and that a considerable, but lower, number of these birds can be restored into the breeding population. There seem to be delays in the restoration of some individual penguins. Results indicate that rehabilitating young penguins is less successful and considerably more expensive than restoring adults to the breeding population.

The conservation value of de-oiling contaminated wildlife has been questioned by several conservation biologists on the basis of negligible survival rates of de-oiled birds; these authors have concluded that de-oiling has made no appreciable contribution to the wild populations of un-oiled birds (Swennen 1977, Boersma 1995, Sharp 1996, Wernham *et al.* 1997, Estes 1998). The one exception to these findings was the earlier South African data on the rehabilitation of African Penguins (Morant *et al.* 1981). On the basis of these findings Sharp (1996) and others (Clark 1984, Boersma 1995, Estes 1998) have regarded the de-oiling of contaminated seabirds as serving only humanitarian and public relations purposes. Some have even argued that investing in oiled wildlife rehabilitation may be detrimental if it diverts limited resources away from more important conservation issues faced by the affected species, and provides the public false perceptions about the real impacts of oil spills and the mitigation value of de-oiling contaminated individuals (Boersma 1995, Estes 1998).

The South African findings contradict Sharp's (1996) conclusions, at least in terms of Cape Gannet survival after the *Castillo de Bellver* spill and of African Penguins de-oiled following the *Apollo Sea* and subsequent spills. For African Penguins these findings indicate substantially better rehabilitation and restoration rates than those previously presented (Morant *et al.* 1981). Penguins may be considered easier to rehabilitate than other seabirds because of their ability to fast for relatively long periods, a feature which is necessary during their annual moult (Adams & Brown 1990). They also tend to make landfall as soon as they become oiled (Underhill *et al.* 1999), thus reducing their exposure and making them relatively easy to capture. The South African findings for Cape Gannets show that the conservation value of de-oiling extends to a volant seabird. Survivors of the *Castillo de Bellver* spill were found to have similar (or slightly lower) survival and restoration rates compared with un-oiled birds (Altwegg *et al.* submitted). Moreover, by 2000 the release rates of de-oiled gannets from SANCCOB were comparable to those of de-oiled African Penguins (Parsons & Underhill 2005).

The better rehabilitation and restoration success rates in South Africa compared with de-oiling operations in the northern hemisphere can be attributed to several factors: the body size, age of birds oiled; capture of most oiled birds at breeding colonies, and; in the case of spills reported here, the release of de-oiled birds near their breeding locality. Both the African Penguin and Cape Gannet are large and robust compared with the main species oiled in the northern hemisphere. African Penguins and Cape Gannets range in body mass between 2 125–3 675g and 2 240–3 296g respectively (Maclean 1993), greater than the body mass of Common Murres (560–1 270g), Western Grebes *Aechmophorus occidentalis* (550–1 225g) and Velvet Scoters *Melanitta fusca* (1 200–1 794g) (Cramp 1985, del Hoyo *et al.* 1992), the main northern hemisphere species considered by Sharp (1996) and Wernham *et al.* (1997). The larger body size of South African birds may reduce handling stress, and through possible possession of greater internal reserves, reduce mortality prior to capture for cleaning. The Little Penguin is the smallest member of the penguin family, with mean body masses of 1 172g and 1 048g for males and females, respectively (Dann *et al.* 1995). The smaller size of the Little Penguin compared with the African Penguin may explain why Little Penguins de-oiled following the *Iron Baron* spill had significantly lower survival rates than un-oiled birds (Goldsworthy *et al.* 2000b). However, body mass alone cannot explain species differences in rehabilitation success. De-oiled California Brown Pelicans *Pelecanus*

occidentalis, which have an average mass of 3 450g (Dunning 1993), upon release exhibit significantly lower survival and restoration rates than un-oiled birds (Anderson *et al.* 1996). Age may also be important in enabling birds to survive oiling and de-oiling. The majority of both African Penguins and Cape Gannets in the spills reported here were adults, many with breeding experience. In addition to the greater survival rates of adults relative to juveniles, adult birds are more likely to return to their breeding colonies after release, thereby facilitating re-sighting efforts.

African Penguins and Cape Gannets in the studied spills were released close to their breeding colonies. Many of the oiled northern hemisphere species are migratory and become oiled far from their breeding localities (Wiens 1996, Cadiou *et al.* 2004). Once contaminated birds are de-oiled, they would need to accumulate additional energy (fat) levels to sustain the return flights to their breeding localities. This is likely to exact an energetic cost on northern hemisphere birds not experienced by the more sedentary species, such as the African Penguin and Cape Gannet. The migratory nature of the Magellanic Penguin, a species which is threatened by chronic oil pollution along the southwest Atlantic coast from northern Argentina to southern Brazil, poses similar problems for the rehabilitation of this species (García Borboroglu *et al.* 2006). The situation is exacerbated by the fact that many parts of Argentina's coastline have no road infrastructure or freshwater with which to wash oiled birds (García Borboroglu *et al.* 2006).

The rehabilitation of African Penguins and Cape Gannets affected by spills in South Africa has been aided by two additional factors. Firstly, oiled birds are generally caught and transferred quickly to the cleaning and treatment centre (SANCCOB), which has developed over many years to become a well-established organisation and facility with permanent and experienced staff. Many spills outside of South Africa have occurred at remote localities far from established cleaning centres. Consequently, there have been delays in capturing and treating oiled birds, and appropriate cleaning and treatment facilities have often been lacking (Heubeck *et al.* 2003). The lack of established facilities has also contributed towards the large costs associated with de-oiling seabirds in the northern hemisphere. The cost of de-oiling seabirds and Sea Otters following the *Exxon Valdez* spill included not only the cost of de-oiling and treatment of the affected wildlife, but also the capital cost of building three new rescue centres under crisis conditions

(Jessup 1998). Secondly, monitoring of rehabilitation and restoration is relatively easy at South African localities. The two species reported here breed at relatively few localities most of which are easily accessible to humans. By contrast, many of the seabirds affected by oil pollution in the northern hemisphere are difficult to monitor because they are either solitary breeders with widely dispersed nests, their colonies or nests are inaccessible, and in some cases may only visit colonies nocturnally (Piatt *et al.* 1991). The relatively large sizes of the African Penguin and Cape Gannet allow larger bands to be used, which greatly improves the feasibility of re-sighting efforts.

Results of these post-release monitoring studies have been used to update strategies and protocols related to oil spill response in South Africa, and have thus contributed towards improved outcomes in subsequent spills. Follow-up research after the *Apollo Sea* spill highlighted the significant conservation value of investing in de-oiling African Penguins, and also provided information which benefited the oiled bird response in the *Treasure* spill. This was especially the case in terms of bird care during transport (Chapter Six). It is important that the process of scientific enquiry into the effects of oiling and de-oiling on seabirds continues and grows, and that these insights are continuously translated into the refinement of protocols so that the population-level benefits of de-oiling can be further improved.

The success in the rehabilitation and especially restoration of de-oiled African Penguins and Cape Gannets is encouraging news for these species, which are both classified as Vulnerable (Barnes 2000), and also face a range of other threats. Thus, de-oiling remains a vital conservation management tool for these species, which should continue. However, the success of de-oiling efforts should not mask the overall negative effects of oil spills on seabird populations. Not all rehabilitated birds may subsequently breed, and even those that do have diminished breeding success for extended periods after oiling. Rescue operations result in substantial disturbance to both target and non-target species and may cause habitat damage. Although African Penguins and Cape Gannets represent the two seabird species most affected by oil spills in South Africa, there are other species, mostly cormorants, that are regularly oiled. The proportions of oiled cormorants that have been successfully rehabilitated and restored have been substantially lower than those of penguins and gannets (Crawford *et al.* 2000b, Wolfaardt *et al.* 2004, Parsons & Underhill 2005). This is largely due to their flighty

nature, which does not permit capture until the birds are in compromised physical condition, thus reducing their probability of surviving the de-oiling process. Although cormorants are less susceptible to oiling than penguins, when a large amount of oil is spilt in close proximity to their colonies, they are at greater risk of becoming contaminated. Following the *Treasure* spill about 20% of Bank Cormorants *Phalacrocorax neglectus* at the Robben Island colony died (Crawford *et al.* 2000b). For a species which has recently been reclassified from Vulnerable to Endangered on the basis of ongoing population declines (Barnes 2000, BirdLife International 2004), the loss of this many birds from the third largest extant breeding colony is cause for concern. Prevention of oil pollution, especially in the vicinity of seabird colonies and their foraging areas, must, therefore, be the primary objective. This objective should be complemented by the continued implementation of oiled bird response strategies. Indeed, every effort should be made to improve these strategies and protocols, for penguins and gannets, and for other seabird species in South Africa which have hitherto been less successfully rehabilitated.

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Table 7.1 Seabird species which breed in southern Africa: their numbers and regional conservation status*

Species	No. of breeding pairs	Conservation Status (from Barnes 2000)	References
African Penguin *Spheniscus demersus*	63 000	Vulnerable & endemic	(Hockey *et al.* 2005)
Leach's Storm Petrel *Oceanodroma leucorhoa*	25		(Whittington *et al.* 1999, Whittington & Dyer 2000, Underhill *et al.* 2002)
Cape Gannet *Morus capensis*	156 000	Vulnerable & endemic	(Hockey *et al.* 2005)
White-breasted Cormorant *Phalacrocorax carbo*	2 500		(Crawford *et al.* 1991)
Bank Cormorant *Phalacrocorax neglectus*	3 100	Recently reclassified from Vulnerable to Endangered & endemic	(Crawford *et al.* 1999a, du Toit *et al.* 2003, BirdLife International 2004)
Cape Cormorant *Phalacrocorax capensis*	72 000	Near-threatened & endemic	(Crawford 1999)
Crowned Cormorant *Phalacrocorax coronatus*	2 700	Near-threatened & endemic	(Crawford *et al.* 1982)
Great White Pelican *Pelecanus onocrotalus*	650	Near-threatened	(Crawford *et al.* 1995a)
Caspian Tern *Sterna caspia*	250	Near-threatened	(Cooper *et al.* 1992)
Swift Tern *Sterna bergii*	6 300	Endemic subspecies	(Crawford 2003, Hockey *et al.* 2005)
Roseate Tern *Sterna dougalli*	250	Endangered	(Crawford *et al.* 1991, Barnes 2000)
Damara Tern *Sterna balaenarum*	4 000	Endangered & endemic	(Simmons 1993, Barnes 2000)
Kelp Gull *Larus dominicanus*	25 500	Endemic subspecies	(du Toit *et al.* 2003, Hockey *et al.* 2005)
Hartlaub's Gull *Larus hartlaubii*	13 000	Endemic	(Williams *et al.* 1990, Crawford *et al.* 1991)
Greyheaded Gull *Larus cirrocephalus*	36		(Crawford *et al.* 1991)

* Only coastal populations for those species which also breed inland

Table 7.2 The number of oiled seabirds admitted to SANCCOB from 2001-2005, a period with no large oil spill incidents. The southern African breeding status of each species is provided: B = Breeder; NB = nonbreeding visitor

Common Name	Species	Breeding status	Number admitted	Proportion (%)
African Penguin	*Spheniscus demersus*	B	2500	86.12
Cape Gannet	*Morus capensis*	B	223	7.68
Cape Cormorant	*Phalacrocorax capensis*	B	35	1.21
Crowned Cormorant	*Phalacrocorax coronatus*	B	5	0.17
White-breasted Cormorant	*Phalacrocorax carbo*	B	2	0.07
Great White Pelican	*Pelecanus onocrotalus*	B	1	0.03
Hartlaub's Gull	*Larus hartlaubii*	B	16	0.55
Kelp Gull	*Larus dominicanus*	B	13	0.45
Swift Tern	*Sterna bergii*	B	101	3.48
Subantarctic Skua	*Catharacta antarctica*	NB	1	0.03
White-chinned Petrel	*Procellaria aequinoctialis*	NB	2	0.07
Pintado Petrel	*Daption capense*	NB	1	0.03
Wilson's Storm Petrel	*Oceanites oceanicus*	NB	1	0.03
Great Shearwater	*Puffinus gravis*	NB	1	0.03
Cory's Shearwater	*Calonectris diomedea*	NB	1	0.03

Table 7.3 Major tanker wrecks and oil spills in South Africa, 1953-2000, and the approximate number of seabirds affected. Updated from Whittington (2002).

Year	Vessel/Source	Location	Cause	Tonnes of oil spilt	Birds oiled
1953	Unknown[1]	Robben Island	Unknown	Unknown	1200 penguins, 700 gannets
1968	*Esso Essen*[2]	Cape Point	Wrecked	15 000	3000 penguins
1970	*Kazimah*[3]	Robben Island	Wrecked	1000+	559 penguins
1971	**Wafra*[4]	Cape Agulhas	Wrecked	10 000	1200+ penguins
1972	Unknown[5]	Dassen Island	Unknown	Unknown	4 000 penguins, 130 Bank Cormorants, < 100 gannets
1972	*Oswego Guardian & Texanita*[2,4]	Ystervark Point	Collision	10 000	1600 penguins
1974	*Oriental Pioneer*[4]	Struisbay	Wrecked	200	500+ penguins
1977	**Venpet & Venoil*[4,6]	Cape St Francis	Collision	31 000	*c.* 47 penguins
1978	*Pantelis A. Lemos*[4]	Near Vondeling Island	Wrecked	300	27 penguins
1983	**Castillo de Bellver*[7,8]	Saldanha Bay	Wrecked	160 000+	5000 gannets
1985	*Kapodistrias*[9]	Cape Recife	Wrecked	100+	923 penguins. 60 gannets
1994	*Apollo Sea*[10]	Dassen Island	Wrecked	2 400	10 000 penguins
1995	Unknown[11]	Near Dyer Island	Unknown	Unknown	1300+ penguins
1996	*Cordigliera*[12]	Transkei Coast	Wrecked	884	1300 penguins
1998	Pipeline spill[13]	Cape Town Harbour & Table Bay	Burst pipeline	150 in harbour, 5 in Table Bay	563 penguins, 150 cormorants
1998	Unkown[12]	Near Malgas Island	Unknown	Unknown	300 gannets
1999	Unkown[12]	Near Malgas Island	Unknown	Unknown	220 gannets
2000	*Treasure*[14]	North of Robben Island	Wrecked	1400	19 000 penguins, 50 cormorants, 30 gannets

*One of world's top 50 spills as measured by the volume of oil spilt (Daidola 1995)

For comparison, the *Exxon Valdez* spilt approximately 36 000 tonnes of crude oil (Garshelis 1997)

Sources:

[1]Rand (1970); [2]Moldan & Westphal (1994); [3]Cooper (1971) [4]Morant *et al.* (1981); [5]Cooper (1972); [6]Moldan *et al.* (1979); [7]Berruti (1987); [8]Moldan *et al.* (1985); [9]Randall & Randall (1986); [10]Erasmus (1995); [11]Whittington(2002); [12]SANCCOB, unpubl. data; [13]Whittington (2000); [14]Crawford *et al.* (2000b)

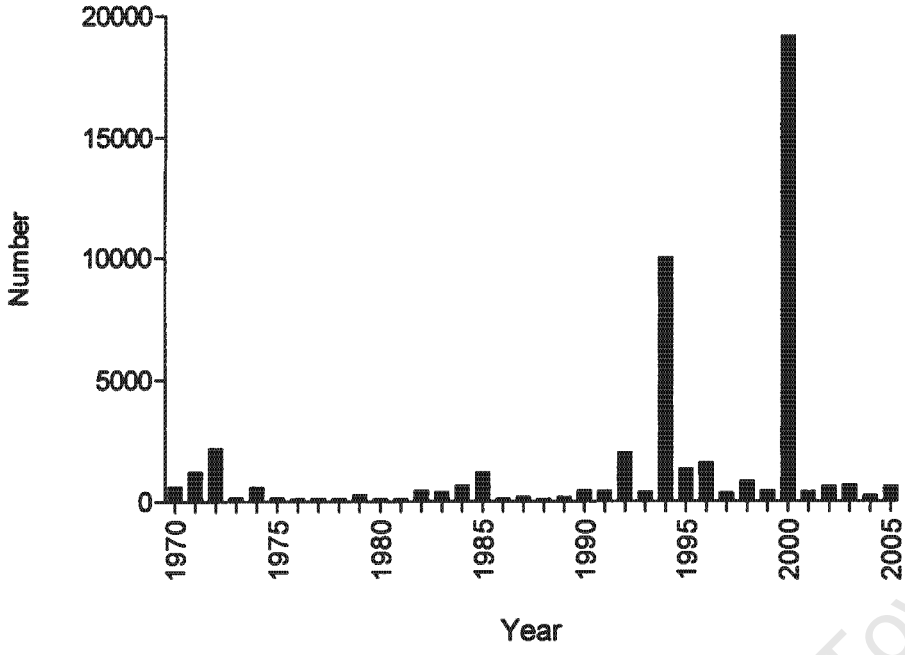

Figure 7.1. Number of oiled African Penguins admitted to SANCCOB, 1970-2005. Updated from Nel *et al.* (2003).

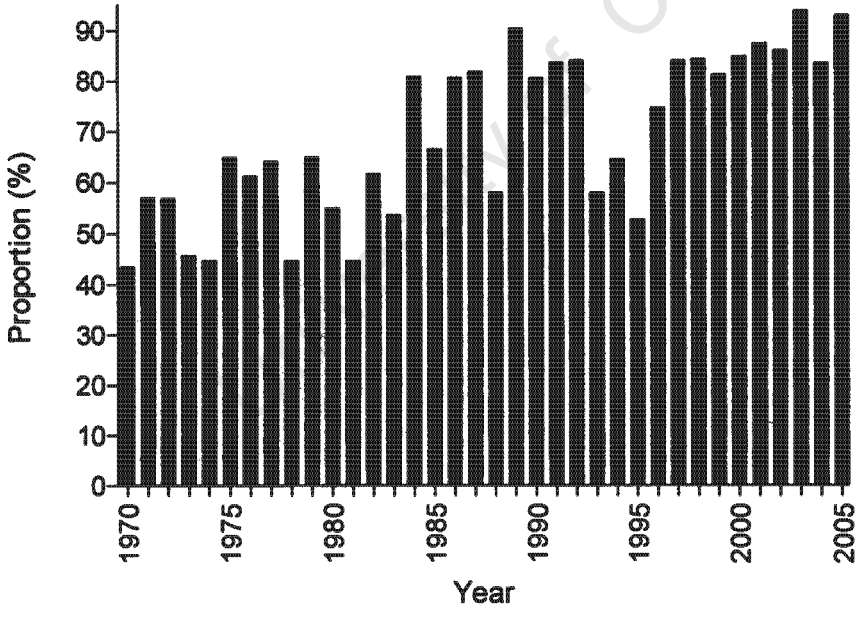

Figure 7.2. Proportion of oiled African Penguins admitted to SANCCOB that were successfully released after de-oiling, 1970-2005. Updated from Nel *et al.* (2003).

Chapter Eight

Conclusions and synthesis

Conclusions and synthesis

The global population of African Penguins *Spheniscus demersus* decreased by 90% during the 20th century (Crawford *et al.* 2001, Kemper *et al.* 2001), leading to its current classification of "Vulnerable" in the regional and international Red Lists (Barnes 2000, BirdLife International 2004, IUCN 2006). At the outset of the 21st century, oiling is considered to be one of the major threats to African Penguin populations (Nel & Whittington 2003, Hockey *et al.* 2005). Vigorous and ongoing debate about the impacts of oil pollution on seabird populations and the role and value of de-oiling as a conservation tool reflects the difficulty of drawing general conclusions about these issues. The findings of this thesis have led to a better understanding of the threat posed by oiling to African Penguins and the conservation value of de-oiling contaminated birds.

Between 1970 and 2005 the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) treated over 45 000 oiled African Penguins, an average of 1 250 per year (Chapter Seven). Although larger numbers of Magellanic Penguins *Spheniscus magellanicus* are oiled annually as a result of chronic oil pollution (Perkins 1983, Boersma 1987, Boersma *et al.* 1990, Gandini *et al.* 1994, García Borboroglu *et al.* 2006), based on the proportion of the global population which has been affected by oil spills, the African Penguin can be considered the bird species most impacted by oil pollution. The demographic traits of African Penguins (relatively low fecundity, deferred sexual maturity and relatively high adult survival) exacerbate the negative impacts of oil mortality on populations. The majority (>75%) of African Penguins oiled have been adult birds (Chapter Seven). For long-lived birds, such as the African Penguin, an increase in adult mortality results in a more rapid decrease in population size than for shorter-lived species (Weimerskirch *et al.* 1987, Croxall & Rothery 1991, Hamer *et al.* 2002). In the context of oiling, one way to reduce adult mortality is to de-oil birds which become contaminated. The conservation value of this intervention depends on the proportion of birds that survive to reproduce, and how successfully they reproduce relative to unaffected individuals.

REHABILITATION SUCCESS

Almost all de-oiled penguins which survive the de-oiling process to be released are rehabilitated (i.e. survive in the wild for at least one month). Differences in the re-sighting rates of de-oiled penguins at different colonies and after different spills are mostly the result of variable re-sighting effort, but may also be influenced by local conditions (e.g. predation pressures), and possible differences in the nature of the oil spill (Chapter Seven). On the basis of the rehabilitation results, it has been estimated that the African Penguin population in 2002 was 19% larger than it would have been had de-oiling not taken place since the establishment of SANCCOB in 1968 (Ryan 2003). Similarly, de-oiled Cape Gannets *Morus capensis* survive at almost the same rate as un-oiled birds (Altwegg *et al.* submitted).

RESTORATION SUCCESS

This study demonstrated substantially greater rates of restoration (proportion of de-oiled birds recorded breeding subsequent to their release) than were reported from earlier studies of de-oiled African Penguins (e.g. Randall *et al.* 1980, Morant *et al.* 1981), and for any other species. The higher rate of restoration (74% of de-oiled birds that were recorded at Dassen Island) compared with the earlier studies of African Penguins probably reflects the systematic and long-term approach (10.5 years of systematic post-release monitoring) adopted in this study compared with the less rigorous studies carried out in the 1970s, which were generally of an opportunistic nature. The improved results may also, in part, have been influenced by advances in the stabilisation and management of oiled birds since the 1970s, as inferred by the improved release rate of de-oiled African Penguins from SANCCOB (Nel & Whittington 2003, Parsons & Underhill 2005, Chapter Seven).

De-oiled juvenile penguins exhibited lower restoration rates than adult birds (Chapters Two and Six). However, this reflects the naturally lower annual survival rate of first-year birds relative to adults (Randall 1983, La Cock *et al.* 1987, Whittington 2002), and an age at first breeding of about four years (Whittington *et al.* 2005), rather than more

profound effects of the oil contamination and de-oiling process *per se* on juveniles than adults.

Although the majority (74%) of rehabilitated birds were successfully restored into the breeding population, the remainder (26%) appear to have been unable to breed. Nonbreeding in this context is permanent and so is distinct from temporary nonbreeding or intermittent breeding. Intermittent breeding (i.e. nonbreeding in individuals that bred previously and are alive (Cam *et al.* 1998)), is a characteristic feature of African Penguin demography, thought to be an adaptive strategy to preserve residual reproductive value (Crawford *et al.* in prep.). Thus, African Penguins are "prudent parents" (Drent & Daan 1980), that would refrain from breeding during periods where the cost of reproduction is likely to reduce the number of subsequent years in which the bird could attempt breeding. Although no research has been conducted to provide evidence that intermittent breeding in African Penguins leads to increased survival and thus increases in the residual reproductive value, the proportion of adult penguins breeding at Robben Island from 1988–1995 was positively correlated with the spawner biomass of Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax* (Crawford *et al.* 1999). This suggests that a greater proportion of the population refrain from breeding when conditions are unfavourable, thereby avoiding the increased costs of reproducing during these periods. However, it has also been suggested that nonbreeders are lower quality individuals (Harris & Wanless 1995, Cam *et al.* 1998).

Because of the 10.5 year study period and its intensity, I should have detected most breeding attempts of de-oiled nonbreeders, even if they bred on only a few occasions. Moreover, in contrast to breeders, permanent nonbreeders spent most of their time along the coastline, rather than in the breeding colonies. It is likely that oiling inhibited breeding in a proportion (26% in the case of de-oiled *Apollo Sea* birds) of the de-oiled birds that returned to their breeding colony. The exact mechanism involved is not clear, but oiling has been found to damage key organs such as the liver and kidney (Fry & Lowenstine 1985), compromise the immune system of affected birds (Briggs *et al.* 1996, Briggs *et al.* 1997) and inhibit and reduce breeding in several other seabirds (Ainley *et al.* 1981, Fry *et al.* 1986, Fowler *et al.* 1995, Giese *et al.* 2000).